Differential effects of environmental factors on ecology of brachiopods and bivalves during the Late Triassic and Jurassic

430 pages, 189 figures, 46 tables

Dissertation zur Erlangung des naturwissenschaftlichen Doktorgrades der
Bayerischen Julius-Maximilians-Universität Würzburg

vorgelegt von

ADAM TOMAŠOVÝCH

aus

Pezinok

Würzburg, April 2006

Eingereicht am: 17.05.2006

1. Gutachter der Dissertation: Prof. Franz T. Fürsich

2. Gutachter der Dissertation: Prof. Markus Wilmsen

Ehrenwörtliche Erklärung

Hiermit erkläre ich, dass die Dissertation selbständing angefertig wurde und keine anderen als die angegebenen Quellen und Hilsmittel benutzt wurden.

Würzburg, 30. 04. 2006

Adam Tomašových

Content

1. Introduction

Rhynchonelliformean brachiopods represent one of the most abundant fossil invertebrate groups with excellent fossil record dating back to Ordovician and ranging up to present. Their evolutionary and ecologic history is characterized by high diversity and abundance during the Paleozoic, and low diversity and restricted occurrence in the present-day oceans. Various macroevolutionary and macroecologic approaches were used to address the Phanerozoic decline of brachiopod abundance and diversity. Sepkoski (1979, 1984) argued that brachiopods shared their ecology (e.g., environmental preferences and competitive abilities) and diversity history with other "Paleozoic" benthic fauna. If it is assumed that the Phanerozoic diversity trajectory can be described by coupled logistic equations, Phanerozoic history of brachiopods (i.e., a substantial component of the "Paleozoic" fauna) could be partly explained by negative interactions with members of the "Modern" benthic groups (e.g., molluscs) that were characterized by higher carrying capacities. However, Courtillot and Gaudemer (1996) argued that the diversity trajectory can be better approximated by non-interactive, logistic diversifications interrupted by mass extinctions. In addition, Alroy (2004) showed that the groups belonging to the "Paleozoic" and "Modern" faunas did not share coherent diversity trajectories. Instead, he suggested that the main evolutionary change took place during the mid-Cretaceous and can be equivalent to the Mesozoic marine revolution of Vermeij (1977). Gould and Calloway (1980) analyzed global generic diversity of brachiopods and stated that their diversity trajectory is mainly a product of the end-Permian mass extinction. In contrast, Sepkoski (1996) re-analyzed diversity of brachiopod genera and suggested that the end-Permian extinction was not a primary factor and biotic interactions with other clades could also shape their diversity trajectory. He also showed that in terms of diversity, brachiopods slightly retreated towards offshore habitats through the Paleozoic, in contrast to expansion of bivalves. These approaches, based mainly on diversity data, give different answers to the question whether the history of post-Paleozoic brachiopods was more affected by unpredictable effects of global and regional mass extinctions (Gould and Calloway, 1980), by long-term direct or indirect biotic interactions with other benthic groups (Vermeij, 1977; Thayer, 1983), or by long-term abiotic environmental changes (Bambach, 1993; Vermeij, 1995).

Instead of tracing diversity fluctuations of brachiopods and bivalves on large temporal and spatial scales, the approach used in this study is to evaluate environmental distribution of brachiopods and bivalves on medium time scales of 100,000 years to several million years in terms of their community-level abundances. The time intervals analysed here are mainly restricted to lithostratigraphic formations corresponding to one or two biostratigraphic zones. The Late Triassic and Jurassic benthic communities are analysed in this study because both brachiopods and bivalves were dominant in level-bottom communities in this time. Since the Cretaceous, community-level abundance of brachiopods was substantially reduced and level-bottom benthic communities were mainly dominated by mollusks. The main motive is to evaluate whether and what environmental factors correlate with replacements between communities dominated by brachiopods and bivalves within restricted time intervals, and whether brachiopods and bivalve guilds substantially differ in their preferences. This task is evaluated with analyses of similarities that explicitly assess (1) whether there is any non-random relationship between community composition one one hand and environmental factors on the other hand, and (2) whether abundance patterns of guilds are non-randomly segregated. This goal should be relevant for understanding evolutionary ecology of brachiopods and bivalves because it is necessary for linking of small-scale population- and metapopulation-level processes with large-scale processes of macroevolution. The presented results should enlighten the role of abiotic vs.

biotic factors in driving the ecologic and evolutionary history of brachiopods and bivalves, and can test whether the Phanerozoic decline in abundance of brachiopods can be explained by their displacement into refugia habitats.

This study is subdivided into several chapters that are devoted to different areas and time intervals. These chapters are relatively independent in their structure and each contain its own abstract, introduction, methods and conclusions. However, these chapters are conceptually linked because they use similar methods and address spatio-temporal turnover of brachiopod and bivalve communities in the Late Triassic and Jurassic. Three chapters are devoted to the Upper Triassic communities derived from the Alps and West Carpathians, three chapters analyse the Lower and Middle Jurassic communities of the High Atlas, one chapter is about the Middle-Upper Jurassic communities of the West Carpathians, and two chapters are focussed on the Upper Jurassic communities of southern Germany and Swiss Jura. One chapter is analysing the effect of the end-Triassic extinction on brachiopod abundances and is showing the role of mass extinction events on brachiopod evolution.

Acknowledgments. I am very thankful to Franz T. Fürsich for supervising, support, enthusiastic and critical discussions, for reviewing of my drafts and manuscripts, and for determinations of bivalves from the Lower and Middle Jurassic of Morocco and the Upper Jurassic of Germany and Switzerland. I thank to Markus Wilmsen for his advice, discussions and reviews, and for introducing me into problems of the Moroccan Jurassic, and to Sarah Niebuhr, Michael Heinze, Gerd Geyer, Michael Schlirf, and Mahmoud Majidifard for their help and advice during my stay in Würzburg. The discussions about the end-Triassic mass extinction with Michael Hautmann, about shell beds with Steffanie Bullrich, and about sequence stratigraphy with Fernando Archuby are appreciated. The field work in the West Carpathians was performed in cooperation with Ján Schlögl, Marián Golej and Jozef Michalík. In addition, Ján Schlögl determined the Middle-Upper Jurassic ammonites of the West Carpahians, and Marián Golej determined bivalves from the Upper Triassic and Middle-Upper Jurassic of the West Carpathians. I am indebted to Günther Schweigert and Gert Bloos for information about localities in southern Germany and for determination of ammonites from the Upper Jurassic, to Milan Sýkora and Roman Aubrecht for information about sections in the West Carpathians, to Mr. Öllinger and Mr. Kaiser for permissions that made the field work in the Saal and Altental sections possible, to Werner Heckendorn (Schümel-Naturschutzstiftung) for permission to work in the Holderbank section, to Driss Sadki for information about the Middle Jurassic sections of Morocco, and to Mohammed Haddane, Larbi Tabit and Fatima Bouyahyaoui for permission of doing field work in the High Atlas. Many thanks go to Thomas D. Olszewski, Susan M. Kidwell, Michał Kowalewski, Sandy Carlson, Alfred Dulai, Attila Vörös, Mike Sandy, Gordon Curry, Lindsey R. Leighton, Daniele Gaspard, Karl W. Flessa, Steve M. Holland, Thomas A. Rothfus, James H. Nebelsick, Jan Kresten Nielsen, Miloš Siblík, Nicole Fraser, Werner Piller, Wolfgang Kiessling and Matthew Collins for their critical reviews of my drafts and manuscripts that were partly related to the chapters presented in this study. I also thank to Michael LaBarbera and Michał Kowalewski for supervising of taphonomic course funded by the University of Washington in 2002, to John Alroy for supervising the course in analytical paleoobiology funded by the National Science Foundation in 2005, and József Pálfy, Steve Hesselbo and Christopher A. McRoberts for the possibility to be funded by the IGCP 458 project and to participate in workshops about the end-Triassic mass extinctions in 2001, 2003 and 2005. This study was supported by the Deutsche Forschungsgemeinschaft (Fu 131/26), DAAD Doctoral Fellowship (2002-2006), the American Association for Petroleum Geologists (2002), the Paleontological Society (2003) and the Systematic Association (2003).

2. Methods

In this chapter, analyses most commonly used in this thesis are explained. Other details and some analyses specific for particular regions and datasets are explained within each chapter in subchapters separately devoted to methods.

Data. The data for this study are represented by eight datasets with sample-level abundances of brachiopod and bivalve species that were sampled in the course of the last four years. These datasets include (1) the Upper Triassic Kössen Formation of the Eastern Alps (65 samples and 7265 specimens), (2) the Upper Triassic Fatra Formation of the West Carpathians (47 samples and 4351 specimens), (3) the Upper Triassic Hybe Formation of the West Carpathians (17 samples and 1709 specimens), (4) the Lower Jurassic Foum Zidet Formation of the Central High Atlas (39 samples and 8536 specimens), (5) the Middle Jurassic Bin El Ouidane and Agoudim formations of the Central High Atlas (118 samples and 8041 specimens,), (6) the Middle-Upper Jurassic formations of the Pieniny Klippen Belt (53 samples and 3716 specimens), (7), the Upper Jurassic formations of southern Germany (94 samples and 7660 specimens), and (8) the Upper Jurassic formations of the Swiss Jura (50 samples and 2570 specimens). Evaluation of effects of the end-Triassic mass extinction on brachiopod communities in the Eastern Alps is based on combined data derived from the Kössen Formation and literature sources. Multivariate analyses were mainly performed on formation-level scales corresponding to biostratigraphic zones or subzones. Therefore, some datasets with long time span were further splitted and evaluated separately.

Data transformations. The role of transformations in multivariate community analyses is mainly related to differential weighting of abundant and rare species in computing the similarities (Clarke and Warwick, 2001). The square root transformation has the effect of down-weighting the importance of highly dominant species, so that similarities depend also on relative abundance of less common species. It can be thought as a rather moderate transformation because the fourth root, logarithmic or presence/absence transformation would lead to more severe down-weighting the effects of abundant species. Analyses of the Late Triassic communities from the Alps were performed with square root-transformed relative abundances (Chapter 3). All other analyses were performed with untransformed relative abundances.

Similarity coefficients. The Bray-Curtis dissimilarities based on untransformed relative abundances were used in the cluster and non-metric multidimensional scaling (NMDS) analyses (Gray et al., 1988; Warwick, 1988; Pandolfi, 1996). The Bray-Curtis similarity (S_{jk}) between the *j*th and *k*th samples is defined as follows:

$$S_{jk} = 100\{1 - \frac{\sum_{i=1}^{p} \left| y_{ij} - y_{ik} \right|}{\sum_{i=1}^{p} \left| y_{ij} + y_{ik} \right|}\},$$

where y_{ij} represents the abundance of the *i*th species ($i = 1, 2, ..., p$) in the *j*th sample ($j = 1, 2, ..., n$) and y_{ik} represents the abundance of the *i*th species in the *k*th sample. In Q-mode analyses, if Bray-Curtis similarity is 100, two samples have identical composition. If it is 0, two samples have no species in common. The Bray-Curtis similarity remains unchanged by inclusion or exclusion of a species which is jointly absent in two samples. In addition, any inclusion or exclusion of a third sample C does not change the similarity between samples A and B. The Bray-Curtis similarity between species *i* and *l* is computed as:

$$S'_{il} = 100\{1 - \frac{\sum_{i=1}^{n} \left| y_{ij} - y_{lj} \right|}{\sum_{i=1}^{n} \left| y_{ij} + y_{lj} \right|}\},$$

where species are compared across all $j = 1, ..., n$ samples. Therefore, in R-mode analyses, if Bray-Curtis similarity is 100, abundances of two genera are the same in all samples; if it is 0, two genera have no samples in common.

Cluster analysis. In this study, the hierarchical agglomerative clustering is used for discrimination of discrete groups of samples with similar species abundances. These groups are termed as sample groups and mostly correspond to the associations of Fürsich (1977) or to the paleocommunity types of Bambach and Bennington (1996). The cluster analysis took the Bray-Curtis similarity as the starting point and successively fused the samples into clusters, starting with the highest pairwise similarities (Clarke and Warwick, 2001). The tree diagram was constructed from the Bray-Curtis similarity matrix by the group-average linking method. For example, the similarity (S) between samples A on one hand and samples B and C on the other hand is the average of S(A, B) and S(A, C). The output of this analysis is presented as a tree diagram or dendrogram. Its y-axis thus represents a similarity level at which two samples or groups of samples were fused. Note that the sequence of samples along the x-axis might not reflect an ordering with respect to their similarity. In contrast to ordination analyses, the cluster analysis does not display relationships among samples along a continuous scale. The clustering can lead to a rather arbitrary sample groups when there is a continuum of compositional change among samples.

Ordinations. An ordination is the term for multivariate analyses that place samples in low-dimensional space so that the relationship among samples reflects (1) their biological similarity (species composition representation), and/or (2) their ordering along environmental gradient (gradient analysis, Digby and Kempton, 1987; ter Braak and Prentice, 1988: De`ath, 1999). These two tasks are related but not completely equivalent and different ordination methods are usually used to solve them.

(1) The species composition representation is mostly solved by non-metric multidimensional scaling (NMDS). NMDS can be especially a preferable ordination method for visualizing the community composition with increasing species turnover along environmental gradients, and with increasing complexity of ecologic gradients that control species abundances (Kenkel and Orlóci, 1986; McCune et al., 2002). NMDS ordinates samples according to their dissimilarity in taxonomic or guild composition. NMDS is used as a dimension-reduction method that effectively reduces multi-dimensional space into low-dimensional ordination space (Kruskal, 1964; Kenkel and Orlóci, 1986; Minchin, 1987). NMDS has a simple concept, leading to a sample map whose inter-sample distances have the same rank order as the corresponding dissimilarities between samples (Clarke and Warwick, 2001). The strength of relationship between inter-sample distances and ranks of dissimilarities is measured by a stress value (“badness of fit”). NMDS does not make any assumptions about the form of the data or the inter-relationship of assemblages (Shi, 1993). In this paper, NMDS was computed with Kruskal`s algorithm (1964) that was repeated twenty times with different random positions of samples in starting configurations.

(2) NMDS does not quantify the length of ecologic gradients as compared to gradient analysis methods, which are based on metric distances rather than on ranks. Correspondence analysis (CA) and its derived rescaled and detrended versions are mainly used in indirect gradient analyses. Detrended correspondence analysis (DCA) performs rescaling of ordination axes so that the spacing of sample (and species) scores along the axes are scaled in units of beta diversity, and detrending to counteract the arch effect that represents an artifact of CA. However, the detrending procedure creates artefactual diamond- or triangle-shaped patterns (Kenkel and Orlóci, 1986; Minchin, 1987). DCA is implicitly based on Chi-square distance matrix and assumes the unimodal response of species distributions along an environmental gradient. Sample scores along the first axis might be highly correlated with environmental gradients (Holland et al., 2001; Scarponi and Kowalewski, 2004; Holland, 2005). The first DCA axis is re-scaled in standard deviation (SD) units. A 50% change in sample composition is approximately recorded as 1-1.4 SD units and a complete turnover correspond to about four SD units (Hill and Gauch, 1980).

Analysis of similarities (ANOSIM). The one-way (one-factorial) ANOSIM tests whether within-group average rank dissimilarity, based on the Bray-Curtis coefficient, is significantly lower than between-group average rank dissimilarity (Clarke and Green, 1988). If the null hypothesis (i.e., there are no differences in composition between groups) is rejected, the differences in composition among groups cannot be explained by chance. The R statistic is calculated as follows:

$$R = \frac{\left(\bar{r}_B - \bar{r}_w\right)}{\frac{1}{2}M},$$

where M = n(n-1)/2 and n is the total number of samples, $\bar{r}_B$ is the average of rank similarities based on all pairs of replicates between different sites, and $\bar{r}_w$ is the average of rank similarities among replicates within sites. The statistical value R potentially ranges from -1 to 1. If it is 1, the groups are completely different in composition; if it is 0, the within-group average rank dissimilarity is not less than the between-group average rank dissimilarity. If it is -1, the rank dissimilarities between groups are invariably smaller than those within habitats. The Monte Carlo randomization is used for estimating the significance level. The R statistic is recomputed so that the sample labels are arbitrarily re-arranged. If there is no consistent difference between sites, this recomputing procedure will on average lead to the R value that is similar to the observed R value. The R value is recalculated for all possible allocation of *n* replicates to *k* samples. In general, there are $(kn)!/[(n!)^k k!]$ distinct ways of permuting the labels of *n* replicates at each of *k* sites. If this number of permutations is too high, the full set of permutations is randomly sampled with replacement to give the null frequency distribution of R. 10000 permutations were performed in this study. If there are more than two factor treatments, the R value shows whether there are any *global* differences among factor treatments. If these differences are significant, particular pairs of factor treatments can be further compared in order to examine where the main between-treatment differences are located. If it is not significant, any further interpretation of results is mostly permissible.

The two-way crossed ANOSIM is an analogue to univariate two-way analysis of variance (ANOVA) and separates effects of two factors by removing the variation caused by one or another factor. In other words, the null hypothesis for the first factor is that there are no differences among samples within each treatment of the second factor, and the null hypothesis for the second factor is that there are no differences among samples within each treatment of the first factor. The null hypothesis for the first factor is examined by a constrained randomisation procedure where an R statistic is calculated separately for each treatment of the second factor (i.e, separated one-way analyses are performed for each treatment) and the resulting R statistics are combined to produce an average statistic R. This average statistic is tested by comparing it with R values from all possible permutations permitted under the null hypothesis. The test is not restricted to balanced designs, although unbalanced designs complicate the averaging of R statistics (Clarke and Warwick, 2001).

95% confidence intervals. The confidence intervals calculated in this thesis were derived from the bootstrapped mean-frequency distribution (resampled with replacements, corresponding to the number of specimens in the sample, and iterated 1000 times). Note that overlap in confidence intervals of two independent means does not always indicate insignificant difference in their mean values. A rule of eye states that for two independent means, when the 95% confidence intervals overlap by about half the average margin of error, the p-value for the comparison of the means is approximately 0.05. When the overlap is zero, the p-value is about 0.01.

3. Brachiopod and bivalve ecology in Late Triassic (Alps, Austria): onshore-offshore replacements caused by variations in sediment and nutrient supply

Abstract. Although onshore to offshore retreat of brachiopods in terms of their community-level abundance took place through the Mesozoic and Cenozoic, this study shows that comparable trend occurred also repeatedly on short-time scale and was mainly driven by variations in sediment and nutrient supply. In the Kössen Formation (Upper Triassic), brachiopods retreat to offshore habitats during nutrient-rich, siliciclastic regime and expand to onshore habitats during nutrient-poor, carbonate regime. Epifaunal bivalves occupy onshore and offshore habitats during both siliciclastic and carbonate regime. Infaunal suspension-feeding bivalves expand to offshore habitats during nutrient-rich, siliciclastic regime and retreat from offshore habitats during nutrient-poor, carbonate regime. The onshore to offshore retreat of brachiopods and the offshore expansion of infaunal bivalves thus repeatedly coincide with the switch from a nutrient-poor, carbonate regime to a nutrient-rich, siliciclastic regime. As brachiopods and epifaunal bivalves were abundant in micrite-rich, soft-bottom habitats, the replacements between infaunal and epifaunal communities cannot be explained by variations in substrate consistency alone. The differences in guild structure between siliciclastic and carbonate regimes and onshore-offshore replacements indicate that distribution of bivalves and brachiopods is related to their differential response to low nutrient supply, turbidity, and possibly oxygen levels. Based on actualistic evidence, brachiopods are able to thrive in nutrient-poor conditions due to their low metabolic demands and are also less tolerant of high turbidity conditions than bivalves. Epifaunal bivalves that co-occur with brachiopods in nutrient-poor habitats may have been characterized by higher clearance rates, in contrast to infaunal bivalves with similar metabolic requirements. Although higher biogenic sediment disturbance or other biotic interactions could play also a significant role in the retreat of brachiopods to offshore habitats, this study highlights the importance of varying nutrient supply and turbidity in governing onshore-offshore replacements on short time-scales.

Introduction

One of the challenges of paleoecology is to resolve and explain disproportional distribution patterns of brachiopods during their Phanerozoic history (Thayer, 1986). Brachiopods were numerically abundant and diverse in Paleozoic habitats and formed an important component of the Paleozoic evolutionary fauna (Thayer, 1983; Sepkoski and Miller, 1985; Alroy, 2004). However, they are fairly restricted in numerical abundance and diversity in communities dominated by the Modern evolutionary fauna in present-day habitats. Although Phanerozoic distribution patterns of brachiopods have not yet been rigorously evaluated, there are two environmental trends and one taphonomic trend, which can be coupled with this trend in brachiopod decline in numerical abundance and diversity (Fig. 1). First, although brachiopods were numerically common in shallow, tropical or subtropical Paleozoic and Mesozoic habitats (e.g., coral reefs or shallow lagoons), it seems that they are now largely restricted to some specific habitats such as shaded fjords, caves or polar regions in modern seas (Jackson et al., 1971; James et al., 1992; Rhodes and Thompson, 1993). Although dense populations of modern brachiopods are locally known from tropical shelf habitats (Kowalewski et al., 2002), the retreat from onshore habitats thus resembles onshore-offshore trends in abundance or diversity observed in several other marine clades (Bottjer and Jablonski, 1988; Aronson et al., 1997). Second, brachiopods were numerically common and diverse in Paleozoic and Mesozoic soft-bottom habitats (Thayer, 1986). In contrast, present-day soft-bottom habitats are rarely dominated by brachiopods in terms of their abundance or diversity, or other immobile epifaunal suspension-feeders such as free-lying bivalves in terms of community-level abundance (LaBarbera, 1981a; Jablonski and Bottjer, 1983). Brachiopods are rather confined to hard-bottom habitats in present-day seas. Although the Paleozoic and modern evolutionary faunas were defined according to their global diversities regardless of their environmental distribution (Sepkoski, 1981), this environmental background indicates that the understanding of community-level history of brachiopods depends also on tracing their environmental preferences. Third, there is a possibility that the decline in numerical abundance and/or diversity of calcitic brachiopods is biased by underrepresentation of aragonitic mollusks due to their higher probability of destruction and lower sampling probability in predominantly lithified, Paleozoic and Mesozoic deposits (Cherns and Wright, 2000, but see Bush and Bambach, 2004; Kidwell, 2005).

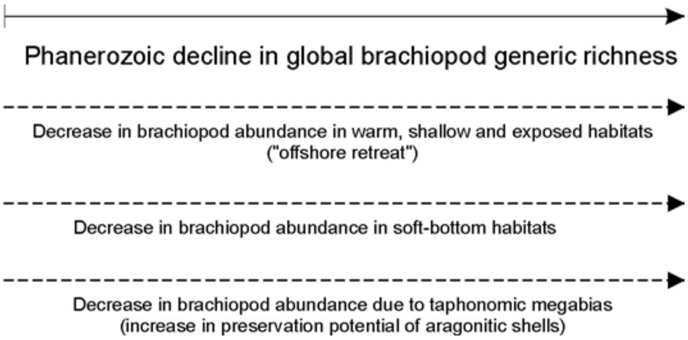


Figure 1–Two simplified trends in environmental distribution of brachiopods and one taphonomic trend, which can be associated with their Phanerozoic decrease in generic richness. It remains to be quantitatively evaluated whether these trends are real and whether they are gradual or stepwise.

Many brachiopod clades, which were diverse and numerically abundant in Paleozoic habitats, went extinct at the end of the Permian. Paleozoic global diversity levels were never re-attained by post-Paleozoic brachiopods (Gould and Calloway, 1980). Although the global diversity trajectories might indicate that the decline of brachiopods has been almost exclusively caused by the end-Permian mass extinction (Gould and Calloway, 1980; Sepkoski, 1996), it seems that this is not supported by their community-level abundances. Brachiopods as a group, represented mainly by rhynchonellids and terebratulids, became again important components in Mesozoic shallow habitats and coral reefs in terms of their community-level abundance (Ager, 1965; Alméras and Elmi, 1993; Aberhan, 1993; Sandy, 1995; Garcia and Dromart, 1997; Fürsich et al., 2001). As diversity and abundance trajectories can be decoupled (McKinney et al., 1998), the end-Permian mass extinction might not be the exclusive cause of subsequent ecologic history of brachiopods. At least, as community-level ecologic success is represented by abundances or biomass rather than by global diversity, the change in community-level abundance and environmental preference of brachiopods between Mesozoic and Cenozoic might not be explained by the end-Permian mass extinction alone. Note brachiopod clades that dominated in shallow habitats and coral reefs during the Mesozoic are more restricted in distribution in present-day seas, indicating that there was a change in their environmental preferences after the end-Permian mass extinction.

There is no consensus, which environmental circumstances allow local proliferation of brachiopods in present-day habitats (Noble et al., 1976; Stewart, 1981; Tunnicliffe and Wilson, 1988; Richardson, 1997; Kostylev et al., 2001; Kowalewski et al., 2002; Barnes and Brockington, 2003). Although the dependence of brachiopods on substrate properties is stressed in paleoecologic analyses (Fürsich et al., 1991; Garcia and Dromart, 1997), it seems that variations in nutrient supply, temperature, oxygen levels and biotic interactions have substantial effects on their distribution. Present-day rhynchonelliformean brachiopods are mainly abundant in polar or cold-temperate regions (Grange et al., 1981; Willan, 1981; Brey et al., 1995; Barnes and Peck, 1997; but see Kowalewski et al., 2002). The latitudinal diversity gradient of rhynchonelliformean brachiopods peaks in temperate latitudes, rather than in the tropics (Walsh, 1996). On one hand, brachiopods are abundant in habitats characterized by an oligotrophic regime or by a regime with seasonally fluctuating nutrients (James et al., 1992). In such habitats limited by low nutrient supply, high metabolic demands of bivalves are supposed to be not fulfilled, whereas the low metabolic demands of brachiopods are (Peck et al., 1987, 1989; Rhodes and Thayer, 1991; Rhodes and Thompson, 1993; Peck, 1996). On the other hand, some occurrences are typical of habitats with high nutrient supply. For example, brachiopods are abundant in plankton-rich fjords of British Columbia (Tunnicliffe and Wilson, 1988), plankton-rich straits of Washington State (Kowalewski et al., 2003), and on a tropical shelf of the Southeast Brazilian Bight that is associated with deep shelf-break upwelling rich in dissolved nutrients (Kowalewski et al., 2002; Rodland et al., 2004). Such nutrient-rich habitats can be characterized by low oxygen levels or relatively cold temperature or other factors which may be another limit for bivalves with high metabolic demands. The actualistic hypothesis about differences in metabolic demands predicts differential abundances of brachiopod and bivalve guilds along nutrient supply, temperature, oxygen or other gradients which increase the cost of a high-energy metabolism. However, quantitative analyses of compositional variations of bivalve and brachiopod communities along an environmental gradient, which could test this actualistic hypothesis hardly exist (e.g., do brachiopods increase in abundance relative to bivalves along a decreasing nutrient supply gradient?).

In order to investigate the co-existence of brachiopods and bivalves in the fossil record, the ideal way is to study the environmental transition from bivalve to brachiopod communities. For this purpose, Late Triassic benthic communities of the Kössen Formation (Northern Calcareous Alps, Austria) are analyzed in this paper. Triassic brachiopods are not yet restricted to refugia habitats, and bivalves are also dominating components of some benthic communities (Fürsich and Wendt, 1977; Laws, 1982; Newton et al., 1987; Stanley et al., 1994; McRoberts et al., 1995, 1997). Note that rhynchonellids and terebratulids were abundant in shallow marine habitats at least until the Early Cretaceous. Although they did not belong to the dominant brachiopods of Late Paleozoic communities, their abundance in Triassic habitats is difficult to explain as a relatively short-term resurgence of otherwise refugia-restricted taxa due released ecologic pressure after the end-Permian mass extinction.

In this paper brachiopod and bivalve communities from the Kössen Formation are analyzed in terms of their taxonomic and guild composition along an onshore-offshore gradient. The goal is to investigate whether their community-level abundance can be explained by substrate variations alone and if their distribution correlates with nutrient supply and turbidity gradients.

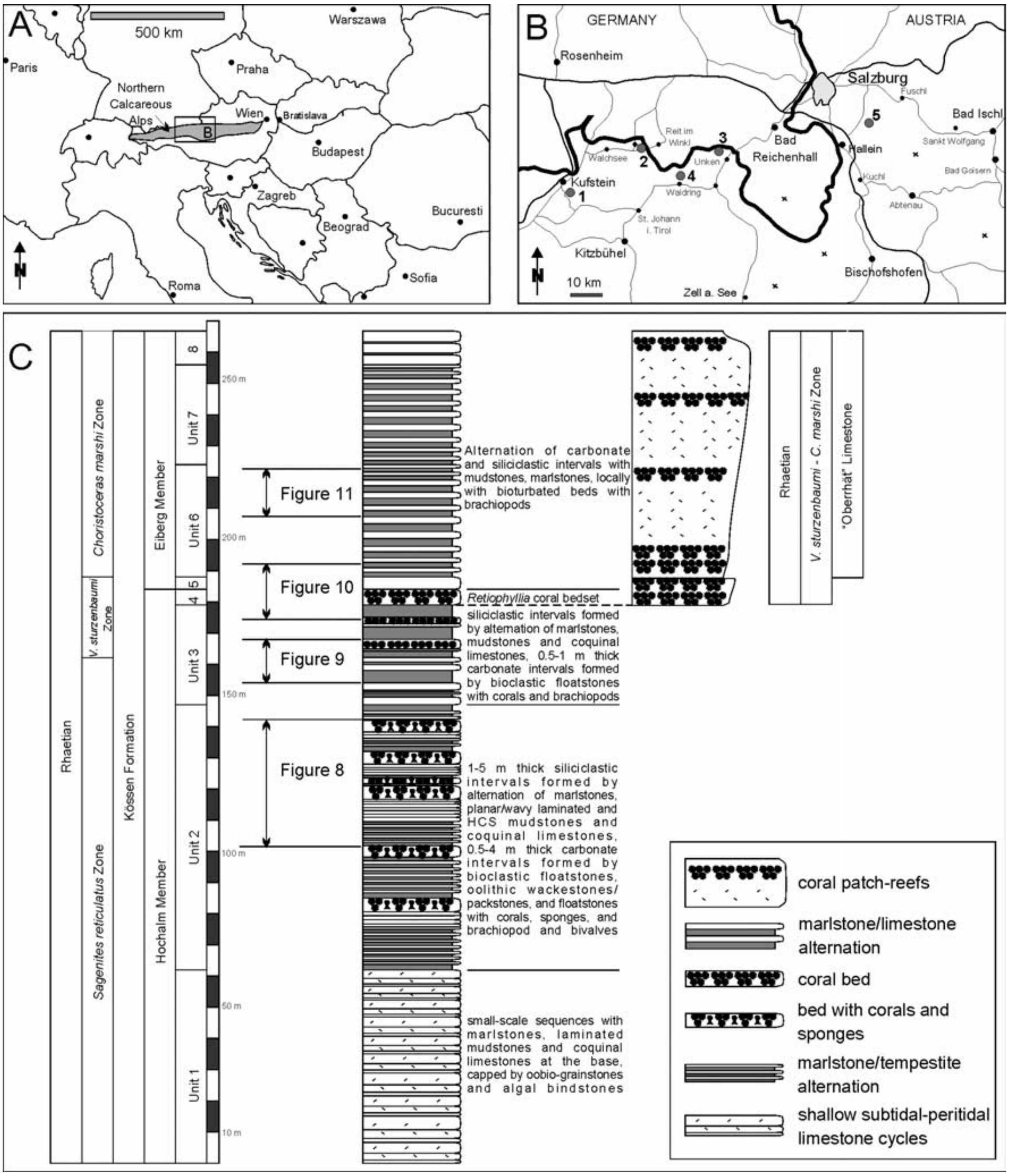


Figure 2– (A) Geographic location of the Northern Calcareous Alps. (B) Geographic location of sections in the Northern Calcareous Alps. (C) Schematic section of the Kössen Formation, with its stratigraphic subdivision based on Golebiowski (1990).

Stratigraphic and environmental framework

Kössen Formation

In the Late Triassic, the depositional area of the Northern Calcareous Alps was situated on the northwestern margin of the Tethys Ocean in the subtropical climatic belt (Haas et al., 1995). The Kössen Formation was deposited in an intra-platform, siliciclastic-carbonate basin, separated from the open ocean by the Dachstein carbonate platform (Kuss, 1983). It consists of two members of Rhaetian age, the lower Hochalm Member and the upper Eiberg Member (Fig. 2). As was shown by Golebiowski (1990) and Holstein (2004), the Kössen Formation records several large-scale depositional trends superimposed on small-scale fluctuations related to sea level and climatic variations. A maximum deepening event is probably recorded in the upper part of the Hochalm Member, where a thick marlstone interval onlaps onto the carbonate platform. A shallowing event is marked by an extensive development of framestones and floatstones with branching and platy corals at the boundary of the two members (Stanton and Flügel, 1989).

The Hochalm Member consists of metre-scale, siliciclastic-carbonate sequences, which are composed of siliciclastic and carbonate intervals (Fig. 3; Golebiowski, 1990). The siliciclastic intervals are formed by alternation of marlstones, mudstones, and thin, simple-event shell beds with planar/wavy mm-scale lamination in their lower part, and abundant limestone beds with hummocky-cross stratification (HCS) in their upper part. The carbonate intervals can be formed by thick limestone beds with corals, sponges and megalodonts, bivalve shell beds and locally oolitic beds in their lower part, and brachiopod-bivalve rudstones, floatstones or pavements in their upper part. The Eiberg Member consists of sequences with marls, marlstones and mudstones, locally with bioturbated wackestones and floatstones, which do not show any signs of storm reworking. Based on thickening-upward limestone beds, asymmetric trend in calcareous/siliciclastic ratio and corresponding variations in palynofacies composition (Hüssner et al., 2000; Holstein, 2004), they can be also subdivided into the siliciclastic and carbonate intervals.

Small-scale sequences

The environmental framework used for testing onshore-offshore patterns in community composition is based on the distribution of the assemblages within the small-scale sequences. The sequences were interpreted by Golebiowski (1991) and Satterley (1996) as shallowing-upward parasequences (Fig. 3) and by Holstein (2004) as asymmetric, transgressive-regressive cycles. Depth-related trends can be inferred from the sequences in the Hochalm Member because they reflect variations in storm intensity and frequency. The sequences in the Eiberg Member are represented by sediments that were deposited below maximum storm wave base. In the Hochalm Member, the occurrence of hummocky-cross stratification in the upper part of the siliciclastic intervals indicates more shallow conditions/higher storm activity in contrast to marlstones and planar/wavy laminated mudstones in their lower part. However, the deposits in the carbonate intervals can commonly show a high proportion of micritic matrix and are indicative of depths both above and below NSWB, i.e., they are not consistently shallower as would be predicted by the shallowing-upward trend. In contrast to the upper part of the siliciclastic intervals which indicate depths above NSWB, some limestone beds in the carbonate intervals indicate depths below NSWB. Therefore, it seems that the carbonate and siliciclastic intervals were deposited at similar bathymetric levels and their vertical replacement does not reflect a simple depth-related trend. In some cases the top of the carbonate interval is characterized by a gradual transition into the following siliciclastic interval, indicating a gradual rather than abrupt increase in siliciclastic input/decrease in carbonate production. A thick marlstone in the middle part of some siliciclastic intervals in Unit 2 may indicate that the sequence did not reach the expected carbonate interval, and the marlstone represents the base of a new sequence. Alternatively, the mid-sequence marlstone represents the maximum deepening event, indicating that there is also a deepening-upward trend at the base of siliciclastic intervals, as indicated by Holstein (2004).

An alternative interpretation of the sequences is that the base of the carbonate interval represents the transgressive surface and its upper part forms a maximum flooding surface in terms of high-frequency depositional sequences (Fig. 3). A third alternative is that the sequences reflect variations in storm frequency and intensity and in rate of siliciclastic and carbonate supply, possibly driven by climatic changes alone (Burgess, 2001). At least four carbonate intervals within Unit 2 and several carbonate intervals in Unit 3 can be traced across the whole Kössen Basin (Golebiowski, 1991), indicating that the onset of carbonate deposition, reflecting conditions favorable for carbonate production, took place relatively rapidly across the whole Kössen Basin.

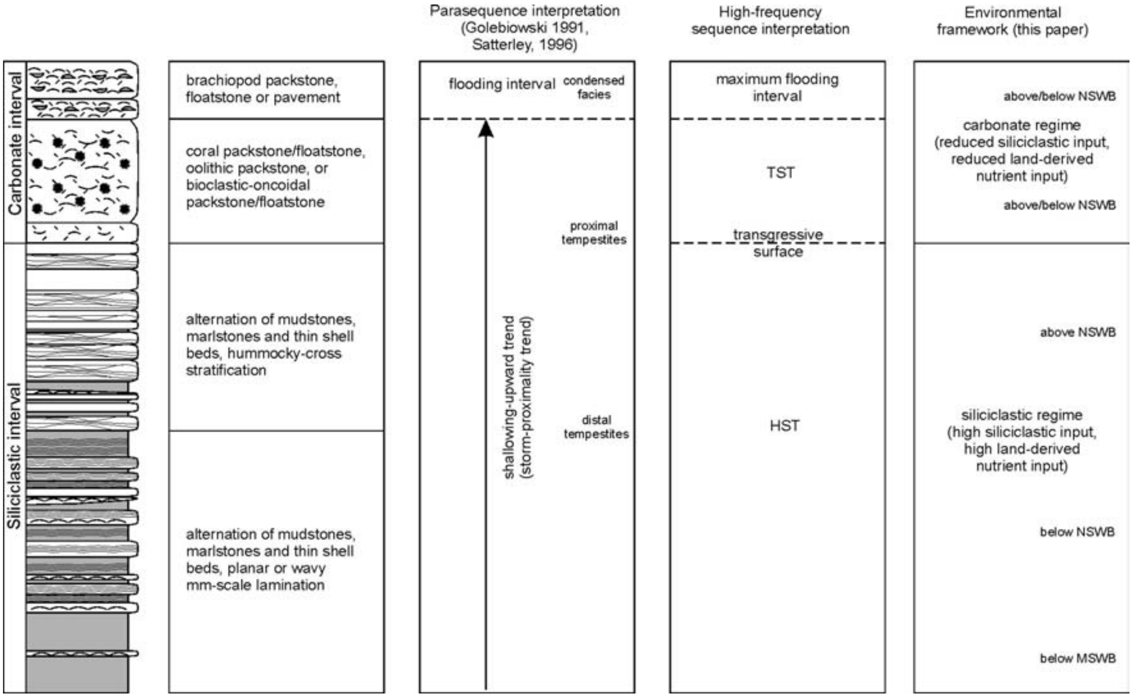


Figure 3 - Schematic section through small-scale, siliciclastic-carbonate sequence with possible interpretations, and environmental framework used in this paper.

For the purposes of this paper, it is assumed that the carbonate and siliciclastic intervals represent two regimes which differed in rate of siliciclastic input and rate of carbonate production. During deposition of the siliciclastic intervals, rate of sedimentation, turbidity levels, and land-derived nutrient supply were thus probably higher than during deposition of the carbonate intervals. In accord with this, Holstein (2004) observed that the carbonate intervals of the Kössen Formation are mostly characterized by low proportions of microplankton, low ratio of continental/marine organic particles and poor preservation of palynomorphs, in contrast to the siliciclastic intervals. The onshore-offshore gradient is thus interpreted from sedimentologic evidence that mainly reflects varying intensity of storm reworking.

Methods

Data analyses

65 samples derived from five sections in the Northern Calcareous Alps (Fig. 2) were analyzed. Although other benthic components as corals, sponges, gastropods and crinoids can locally be present, only brachiopods and bivalves were included in the analyses. All determinable brachiopods and bivalves larger than 2-3 mm were mechanically sampled from lithified or poorly lithified rocks. In addition, nine samples from the dataset of Golebiowski (1989) based on similar sampling protocol were used. The samples encompass the whole Kössen Formation with the exception of its lowermost unit. With the exception of five samples, all samples contain more than 25 specimens (Appendix 1). Although the five samples contain more than ten specimens only, they were also included into the analysis because they contain brachiopod taxa, which are rare or absent in other samples. Taxonomic identifications were based on Pearson (1977), Michalík (1977b), Golebiowski (1989) and Siblík (1998). The absolute abundances were converted into number of individuals with the minimum number of individuals (MNI) approach (i.e., the sum of articulated shells plus dominating number of either dorsal or ventral valves; Gilinsky and Bennington, 1994) and standardized to relative abundances. The MNI approach can be preferable because some bivalves show preferential bias towards one or another valve type.

A cluster analysis was used for identification of sample groups with similar taxonomic composition and relative abundances. The sample groups correspond to the associations of Fürsich (1977) or to the paleocommunity types of Bambach and Bennington (1996). One-way analysis of similarities (ANOSIM) was used for evaluating whether there are differences in species and guild composition among particular habitats. The ANOSIM tests whether within-habitat average rank dissimilarity, based on the Bray-Curtis coefficient, is significantly lower than between-habitat average rank dissimilarity (Clarke and Green, 1988). ANOSIM is complemented by non-metric multidimensional scaling (NMDS), which ordinates samples according to their dissimilarity in species or guild composition. Although NMDS does not quantify the length of ecologic gradients as compared to methods based on metric distances rather than on ranks (e.g., detrended correspondence analysis), it does not make any assumptions about the form of the data or the inter-relationship of assemblages (Shi, 1993). In this study, NMDS was computed with Kruskal`s algorithm (1964) that was repeated twenty times with different random positions of samples in starting configurations.

The Bray-Curtis dissimilarities based on square root transformed relative abundances were used in the cluster and NMDS analyses (Gray et al., 1988; Warwick, 1988; Pandolfi, 1996). The results of this study do not vary substantially when untransformed relative abundances are used. ANOSIM tested the differences in community composition among the following three depth habitats, which were discriminated with sedimentologic evidence: (1) a habitat above NSWB represented by amalgamated packstones and floatstones with signs of sorting, convex-up or stacked valve orientations, internal erosion boundaries and hummocky-cross stratified beds; (2) a habitat between NSWB and MSWB represented by thin layers of simple-event packstones associated with planar/wavy, mm-scale laminated beds in the siliciclastic intervals, and by floatstones and wackestones that reflect alternation of event and background deposits in the carbonate intervals; and (3) a habitat below MSWB with minimal signs of high-energy disturbance, represented by marlstones and mudstones (Appendix 2). Note that this protocol reflects both structures of sampled beds and their sedimentologic context within sequences. For example, if several mm-thick packstone formed by winnowed shell pavement is embedded within homogeneous marlstones, the sample is assigned to the habitat below MSWB. If such pavement alternates with planar/wavy laminated mudstones and other pavements, it is assigned to the habitat between NSWB and MSWB. The testing was performed separately for the carbonate and siliciclastic intervals. If the carbonate and siliciclastic intervals were poorly distinguishable (e.g., as in the upper parts of the Hochalm Member), marlstones were assigned to the siliciclastic intervals and limestones to the carbonate intervals.

Guild assignments

A guild is defined as a group of species that exploit the same class of environmental resource in a similar way (Root, 1967; Simberloff and Dayan, 1991). Bivalve classification into six guilds (i.e., free-lying, cementing, epibyssate, endobyssate, shallow and deep burrowing suspension-feeders, and shallow burrowing deposit-feeders) follows Aberhan (1994). Until now, differences in feeding strategies between bivalves with filibranch, pseudolamellibranch and eulamellibranch gills were hardly considered in paleoecologic analyses (but see McRoberts and Newton, 1995; McRoberts et al., 1995). However, actualistic evidence indicates that the different gill types correspond to the distinct feeding strategies with respect to the quality and quantity of nutrient supply (e.g., they differ in clearance and rejection rates under varying particle concentrations). Therefore, the bivalve guilds were subdivided according to their gill type according to Stanley (1968). The pseudolamellibranch gill is assigned to members of the family Ostreidae (*Actinostreon*). Due to some inevitable correlation between guilds and gill type, only free-lying bivalves are further subdivided into a free-lying filibranch and pseudolamellibranch guild and shallow burrowing bivalves into a shallow burrowing eulamellibranch and a filibranch guild (i.e., cementing, epibyssate, and endobyssate taxa are invariably characterized by filibranch gill, and deep burrowers by eulamellibranch gill, Appendix 3). Brachiopods are differentiated into a pedunculate and a free-lying guild (Alexander, 1977; Thayer, 1983). The rhynchonellids *Calcirhynchia subrimosa* and Rhynchonellid sp. A are assigned to the free-lying guild because they possess highly biconvex shells, secondary shell thickening in the delthyrial and notothyrial cavities, and strongly incurved ventral beak with minute pedicle opening.

Benthic communities

Using group average linkage method, the Q-mode cluster analysis of the exhaustive dataset discriminated 13 sample groups at a Bray-Curtis similarity of approximately 30 (Fig. 4). Six groups are dominated by bivalves and seven groups by brachiopods. Six bivalve sample groups are dominated by infaunal bivalves (*Isocyprina* and *Myophoriopis*), semi-infaunal bivalves (*Bakevellia* and *Gervillaria*), and epifaunal bivalves (*Cassianella* and *Chlamys*). Seven brachiopod sample groups are dominated by pedunculate brachiopods (*Rhaetina gregaria, R. pyriformis, Fissirhynchia*, and *Zugmayerella*) and free-lying brachiopods (*Oxycolpella*, Rhynchonellid sp. A, and *Calcirhynchia*). Relative abundances of species and guilds are shown in Figures 5 and 6.

Sample groups dominated by infaunal bivalves

(1) The *Isocyprina* sample group is represented by eight samples with 3210 individuals. The dominant species is the shallow burrowing *Isocyprina alpina* (60%), followed by the endobyssate *Bakevellia praecursor* (23%), and the deposit-feeding *Nuculana claviformis* (12%). The bivalves *Gervillaria inflata* and *Placunopsis alpina* and the brachiopod *Rhaetina gregaria* are rare (< 5%). This group is limited to the lower part of the siliciclastic intervals of Unit 2. It consistently occurs in thin,

well to moderately sorted and densely packed packstones, or in pavements alternating with mudstones and marlstones, locally with mm-scale planar and wavy lamination.

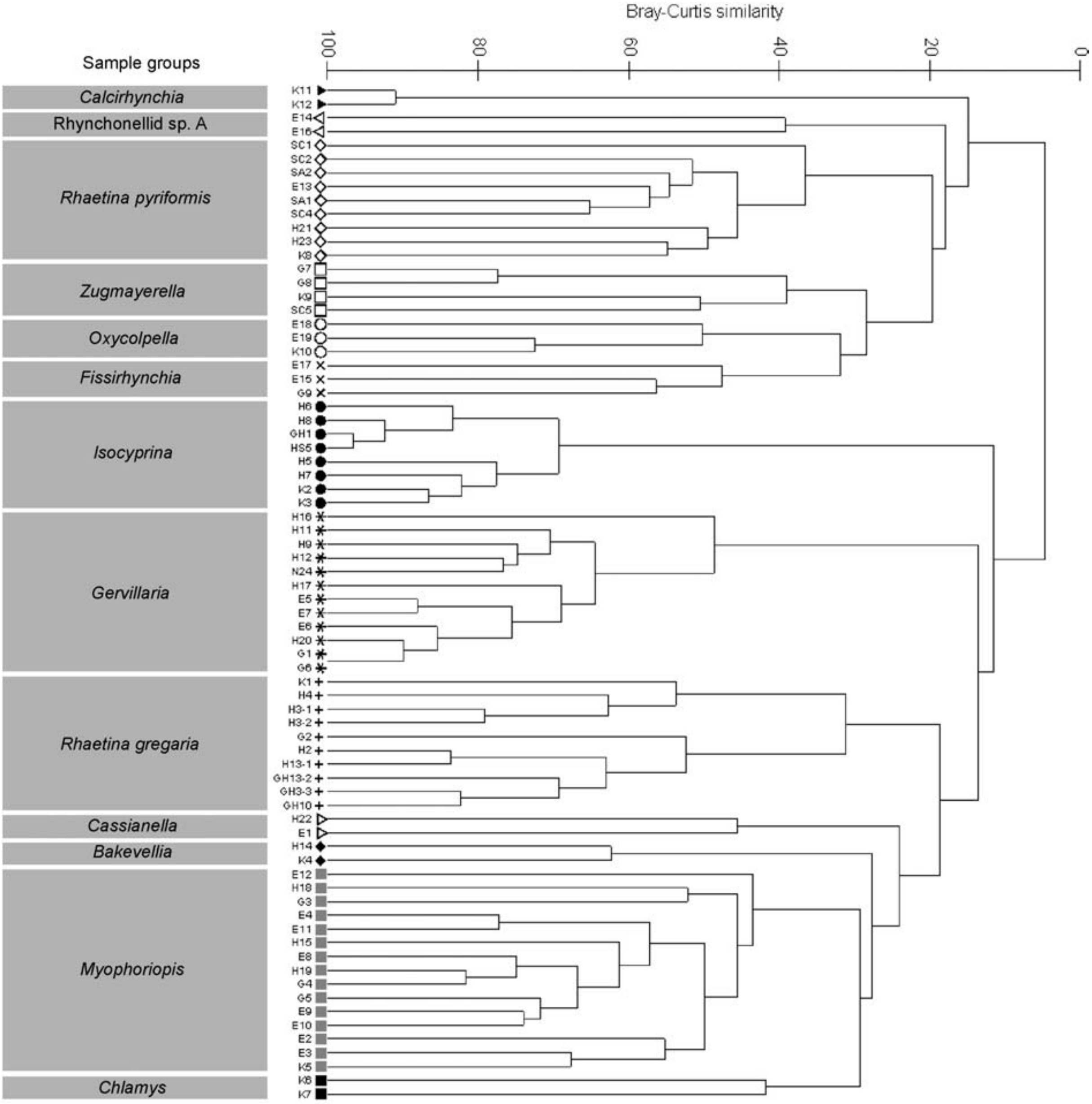


Figure 4 - Cluster analysis of the samples, leading to discrimination of 13 sample groups.

(2) The *Myophoriopis* sample group is represented by 15 samples with 1097 individuals. The shallow burrowing bivalve *Myophoriopis isoceles* (29%) and the epibyssate bivalve *Rhaetavicula contorta* (27%) are the two most dominant species. *Protocardia rhaetica* (11%), *Gervillaria inflata* (8%), *Placunopsis alpina* (7%), and *Pseudocorbula ewaldi* (6%) are less common. This sample group is limited to Unit 3. It occurs mostly in the lower part of the siliciclastic intervals, rarely in their upper part. It is found in marlstones and in thin, well to moderately sorted packstones or pavements. It occurs also in the carbonate intervals in amalgamated packstones and floatstones with complex internal stratification.

Sample groups dominated by semi-infaunal bivalves

(3) The *Bakevellia* sample group is represented by two samples with 127 individuals. It is dominated by the endobyssate bivalve *Bakevellia praecursor* (71%). *Rhaetavicula contorta* is less abundant (19%), *Myophoriopis isoceles* and *Pseudocorbula ewaldi* are rare (< 5%). This group is present in the carbonate intervals or in the upper part of the siliciclastic intervals of Unit 3.

(4) The *Gervillaria* sample group consists of 12 samples with 642 individuals. The endobyssate bivalve *Gervillaria inflata* heavily dominates in this sample group (83%). *Palaeocardita austriaca*, *Placunopsis alpina*, *Modiolus minutus*, and *Liostrea hinnites* may be present. The sample group consistently occurs in upper parts of the siliciclastic intervals of units 2 and 3. It is preserved either as pavements with convex-up oriented valves within hummocky-cross stratified limestone beds, or as several cm-thick, loosely packed floatstones with erosional bases or gutters, with stacked valves. Locally, *Gervillaria* forms clumps in undisturbed marlstones.

Sample groups dominated by epifaunal bivalves

(5) The *Cassianella* sample group is represented by two samples with 125 individuals. The free-lying bivalve *Cassianella inaequiradiata* dominates (75%). The shallow burrowing bivalves *Myophoriopis isoceles* (11%) and *Protocardia rhaetica* (9%) are less abundant. This sample group occurs in marlstones in the upper part of Unit 3.

(6) The *Chlamys* sample group is recognized in two samples with 71 individuals. The epibyssate bivalves *Chlamys coronata* (34%) and *Rhaetavicula contorta* (23%), the shallow burrowing bivalve *Protocardia rhaetica* (14%) and the deep burrowing burrowing *Homomya lagenalis* (10%) are common. This group occurs in bioturbated marlstones of Unit 3. Based on biomass instead of relative abundance, *Homomya* might be the dominant taxon. Golebiowski (1991) named a fossil assemblage of the similar composition as the *Homomya* biofacies.

Sample groups dominated by pedunculate brachiopods

(7) The *Rhaetina gregaria* sample group is represented by ten samples with 979 individuals. The pedunculate brachiopod *R. gregaria* (44%) is most abundant, accompanied by the cementing bivalve *Atreta intusstriata* (29%). *Rhaetavicula contorta* (6%) and *Gervillaria inflata* (6%) are less common. *Palaeocardita austriaca* (3%), *Liostrea hinnites* (3%), and *Chlamys* sp. (2%) are rare. This sample group occurs mainly in the carbonate intervals of units 2 and 3. It is present either in their lower parts in thick floatstone beds with corals, or in their upper parts in bioclastic floatstones, packstones and pavements. Thick limestone beds with corals show high proportions of micritic matrix and locally internal stratification, formed by alternations of thin packstones and floatstones. The floatstones with brachiopods are poorly sorted, loosely packed and bioturbated, with rare features of storm disturbance. The packstones show nesting and stacking of densely packed brachiopod valves, commonly in several, partly amalgamated layers. Locally, this sample group occurs in the lowermost part of the siliciclastic intervals in thin shell beds intercalated between marlstones, below the first appearance of the *Isocyprina* sample group.

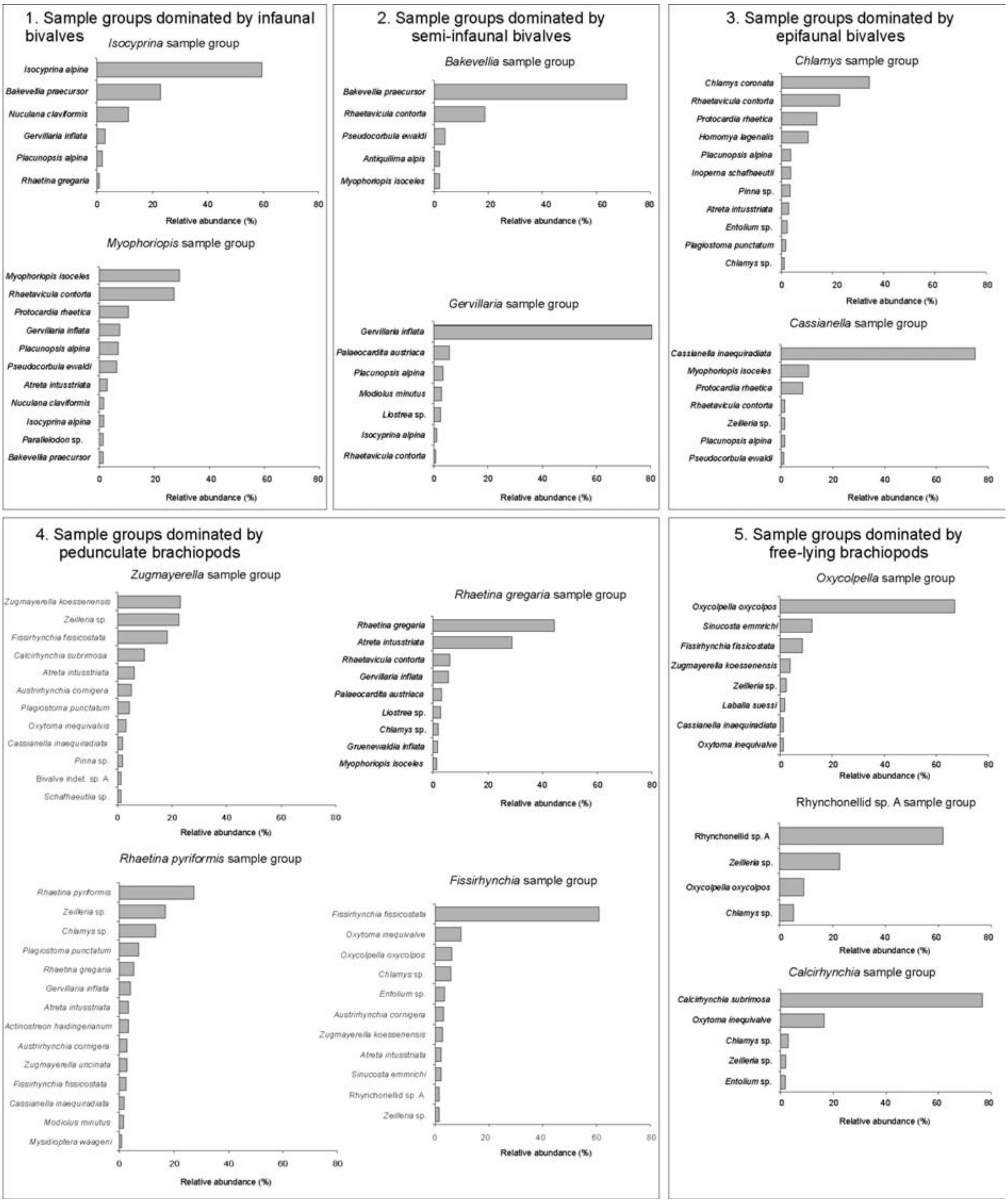


Figure 5 - Relative abundances of species in the 13 sample groups. Species < 1% are excluded.

(8) The *Rhaetina pyriformis* sample group is represented by nine samples with 436 individuals. The pedunculate brachiopods *R. pyriformis* (28%) and *Zeilleria* sp. (17%) dominate, followed by *Chlamys* sp. (13%). *Plagiostoma punctatum* (7%) and *Rhaetina gregaria* (5%) are less common. Other pedunculate brachiopods (*Austrirhynchia cornigera, Zugmayerella uncinata, Fissirhynchia fissicostata*) and bivalves (*Gervillaria inflata, Atreta intusstriata, Actinostreon hadingerianum*) are rare. Shallow and deep burrowers are scarce (2%). This sample group consistently occurs in 20-30 cm thick, coral-debris, micritic-rich floatstones with little signs of storm-reworking, or in coral framestones in the upper part of Unit 3 and in Unit 4. In coral framestones, brachiopods and bivalves are present as interstitial fauna among coral branches, or they occur in sediment which fills pockets among coral thickets.

(9) The *Fissirhynchia* sample group consists of three samples with 164 individuals. The rhynchonellid *Fissirhynchia fissicostata* dominates (61%), followed by the less abundant epibyssate bivalves *Oxytoma inequivalve* (10%) and *Chlamys* sp. (6%), and the free-lying brachiopod *Oxycolpella* (6%). Other brachiopods are represented either by pedunculate (*Zugmayerella koessenensis, Sinucosta emmrichi, Austrirhynchia cornigera, Zeilleria* sp.) or free-lying species (Rhynchonellid A*)*. Infaunal bivalves are absent. This sample group is present in marlstones and mudstones in lower and middle parts of the Eiberg Member.

(10) The *Zugmayerella* sample group is present in four samples with 85 individuals. The pedunculate brachiopods *Zugmayerella koessenensis* (23%), *Fissirhynchia fissicostata* (18%), and *Zeilleria* sp. (22%) are abundant. Free-lying brachiopods (11%), and epibyssate (8%) and cementing bivalves (6%) are less common. This sample group occurs mainly in coral patch-reefs in the Steinplatte and Gaissau sections in Unit 4. These reefs are formed by alternations of framestones with beds of toppled coral colonies and fragmented coral debris. The sample group also occurs in marlstones of the Eiberg Member.

Sample groups dominated by free-lying brachiopods

(11) The *Oxycolpella* sample group consists of three samples with 112 individuals. The free-lying brachiopod *Oxycolpella oxycolpos* (67%) is followed by the less common pedunculate brachiopods *Sinucosta emmrichi* (12%), *Fissirhynchia fissicostata* (8%), *Zugmayerella koessenensis* (4%), *Zeilleria* sp. (3%), and *Laballa suessi* (2%). Bivalves are rare, represented by epibysate, cementing and free-lying guilds. This sample group occurs in marlstones and mudstones of the middle part of the Eiberg Member.

(12) The Rhynchonellid A sample group is represented by two samples with 91 individuals, with a high dominance of the free-lying rhynchonellid A (62%). Other brachiopods are represented by the pedunculate brachiopod *Zeilleria* sp. (23%) and the free-lying brachiopod *Oxycolpella oxycolpos* (9%). The epibyssate bivalves *Chlamys* sp. (5%) and *Oxytoma inequivalvis* (1%) are less common. This sample group occurs in marlstones and mudstones of the middle part of the Eiberg Member.

(13) The *Calcirhynchia* sample group is represented by two samples with 126 individuals. It is dominated by the free-lying brachiopod *Calcirhynchia subrimosa* (77%), followed by the less common epibyssate bivalve *Oxytoma inequivalvis* (17%), and rare *Chlamys* (3%) and *Zeilleria* (2%). This sample groups was found in the middle part of the Eiberg Member.

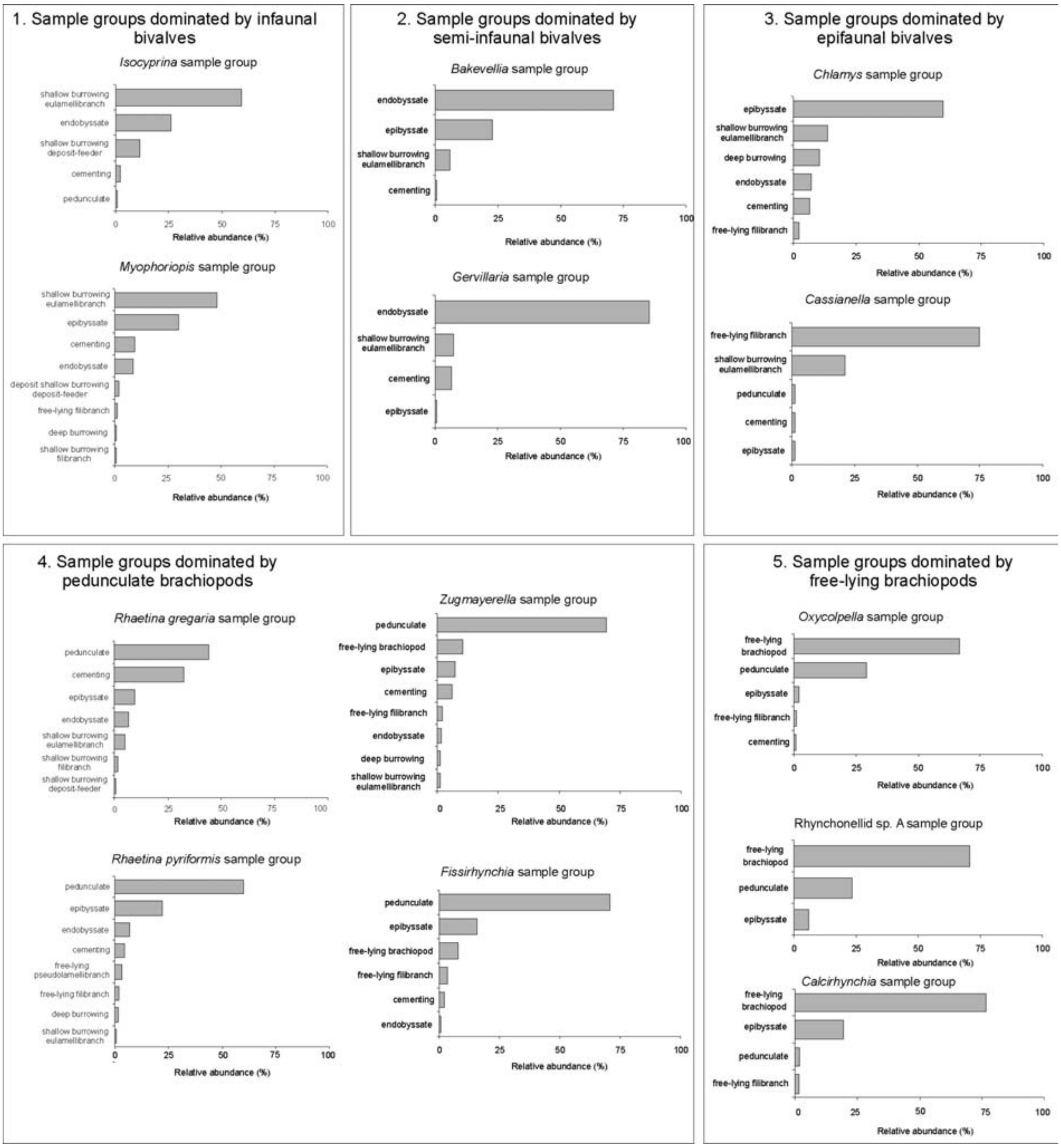


Figure 6 - Relative abundances of guilds in the 13 sample groups. All guilds are shown.

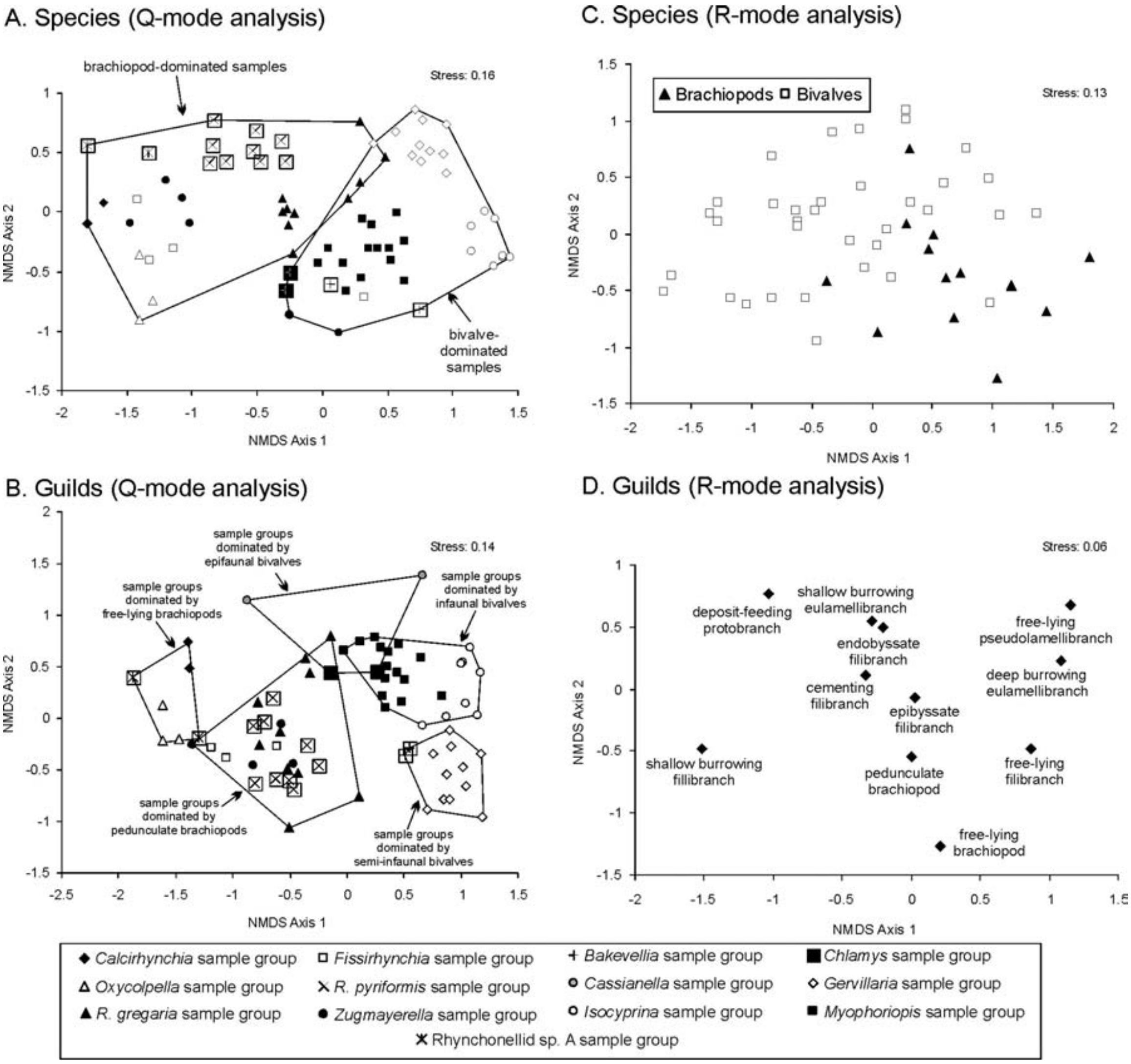


Figure 7 - Non-metric multidimensional scaling (NMDS) analyses. (A) Q-mode analysis of samples based on species composition. (B) Q-mode analysis of samples based on guild composition. (C) R-mode analysis of species. (D) R-mode analysis of guilds.

Ordination of samples, species and guilds

In the Q-mode NMDS based on species composition (Fig. 7A), some sample groups discriminated by the cluster analysis are well segregated (e.g., *Isocyprina, Gervillaria*, and *R. pyriformis* sample groups). However, most of them continuously pass into each other, indicating that the compositional gradient has been arbitrarily dissected into the sample groups. Importantly, brachiopod sample groups show poor overlap with bivalve sample groups. The transitional position between them is occupied by the *Rhaetina gregaria* sample group, which contains some bivalves also occurring in other bivalve and brachiopod sample groups (e.g., *Atreta*, *Rhaetavicula*, and *Gervillaria*). *R. gregaria* occurs also in the brachiopod-dominated *R. pyriformis* sample group. Other brachiopod species occur almost exclusively in brachiopod-dominated sample groups.

Q-mode NMDS based on guild composition shows mostly good separation among the sample groups dominated by different guilds (Fig. 7B), indicating that their differences in guild composition are consistent. The sample groups dominated by free-lying brachiopods are well separated from those dominated by pedunculates. In general, epifaunal bivalve guilds are more common than infaunal and semi-infaunal guilds in brachiopod sample groups. There is also some overlap between the sample groups dominated by pedunculate brachiopods and epifaunal bivalves (Fig. 7B). In turn, the sample groups dominated by epifaunal bivalves show partial overlap with the sample groups dominated by infaunal bivalves. The sample groups with infaunal and semi-infaunal bivalves are also segregated. R-mode NMDS based on species shows that although there is some overlap among bivalve and brachiopod species, brachiopods tend to co-exist more commonly with other brachiopods than with bivalves (Fig. 7C). R-mode NMDS of guilds shows that both pedunculate and free-lying brachiopods co-exist more commonly with epifaunal bivalve guilds than with infaunal or semi-infaunal bivalve guilds (Fig. 7D). In contrast, shallow burrowing eulamellibranch and endobyssate guilds are closely associated.

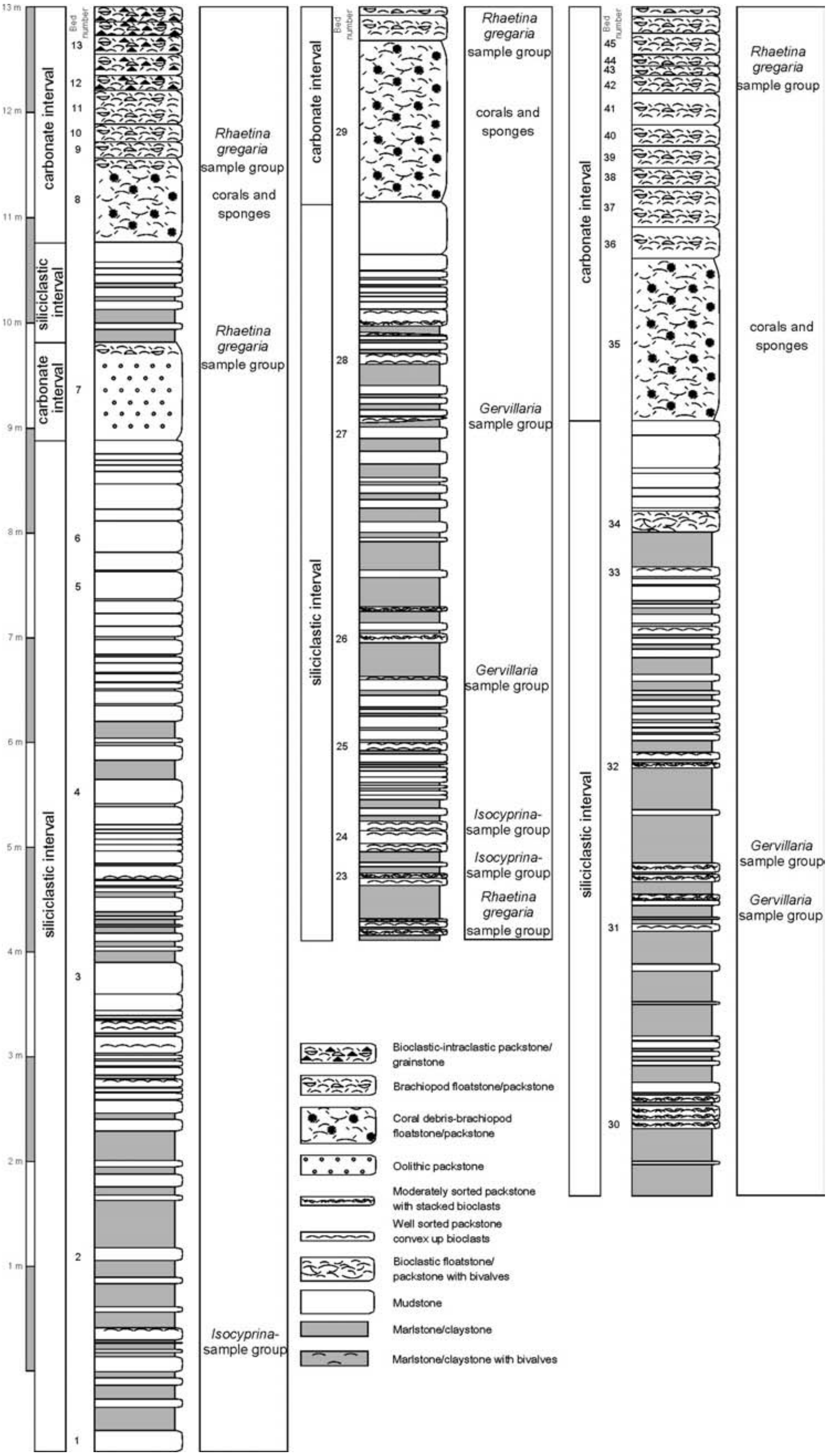


Figure 8 - Stratigraphic distribution of sample groups in Unit 2 of the Hochalm Member. The three segments represent successive parts of the section at Hochalm and record four siliciclastic-carbonate sequences.

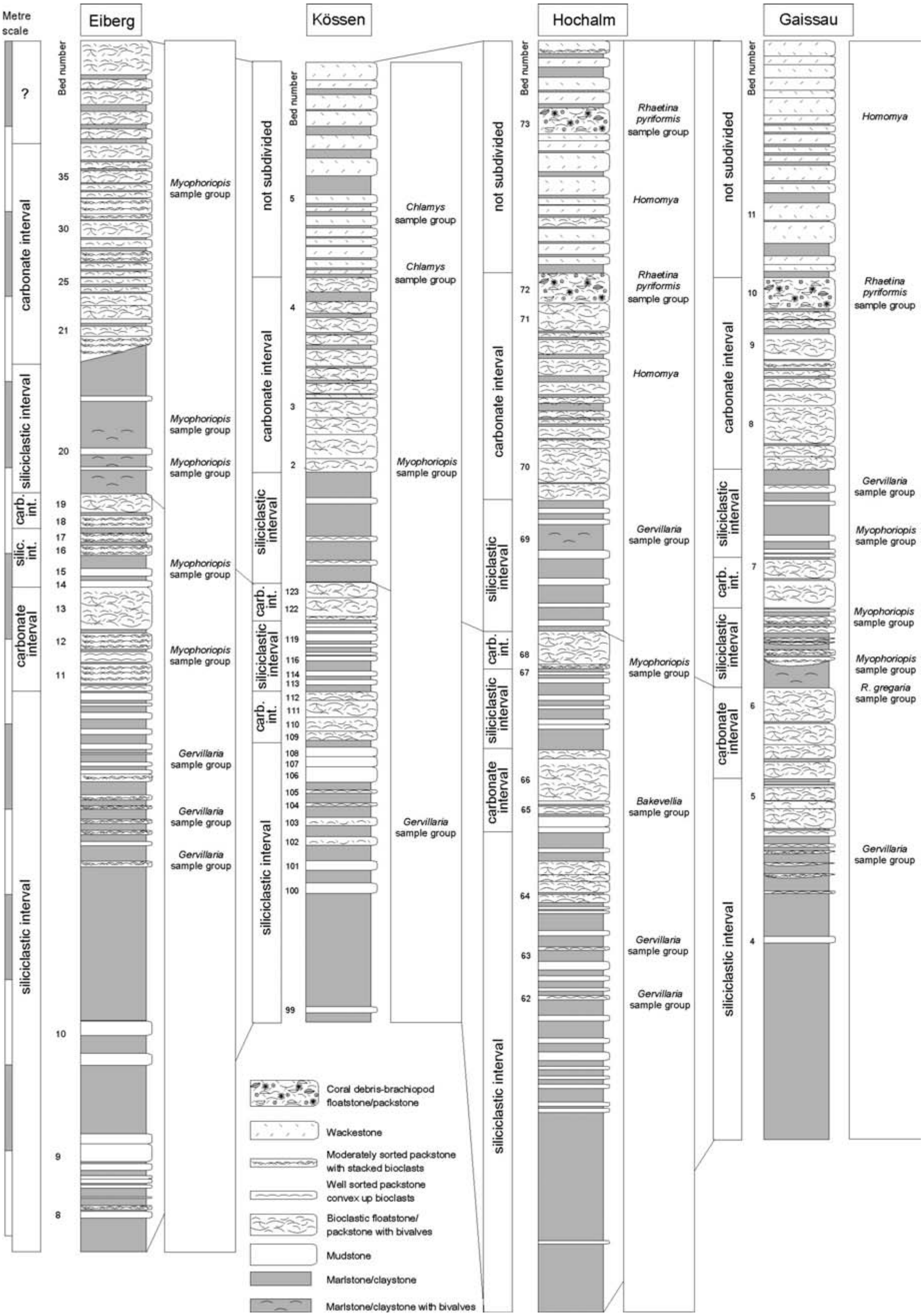


Figure 9 - Stratigraphic distribution of sample groups in Unit 3 of the Hochalm Member. The four sections represent stratigraphically equivalent segments of the lower parts of Unit 3 (see correlation lines). The occurrence of the bivalve *Homomya*, typical of the *Chlamys* sample group, is shown for several beds which were not quantitatively analyzed.

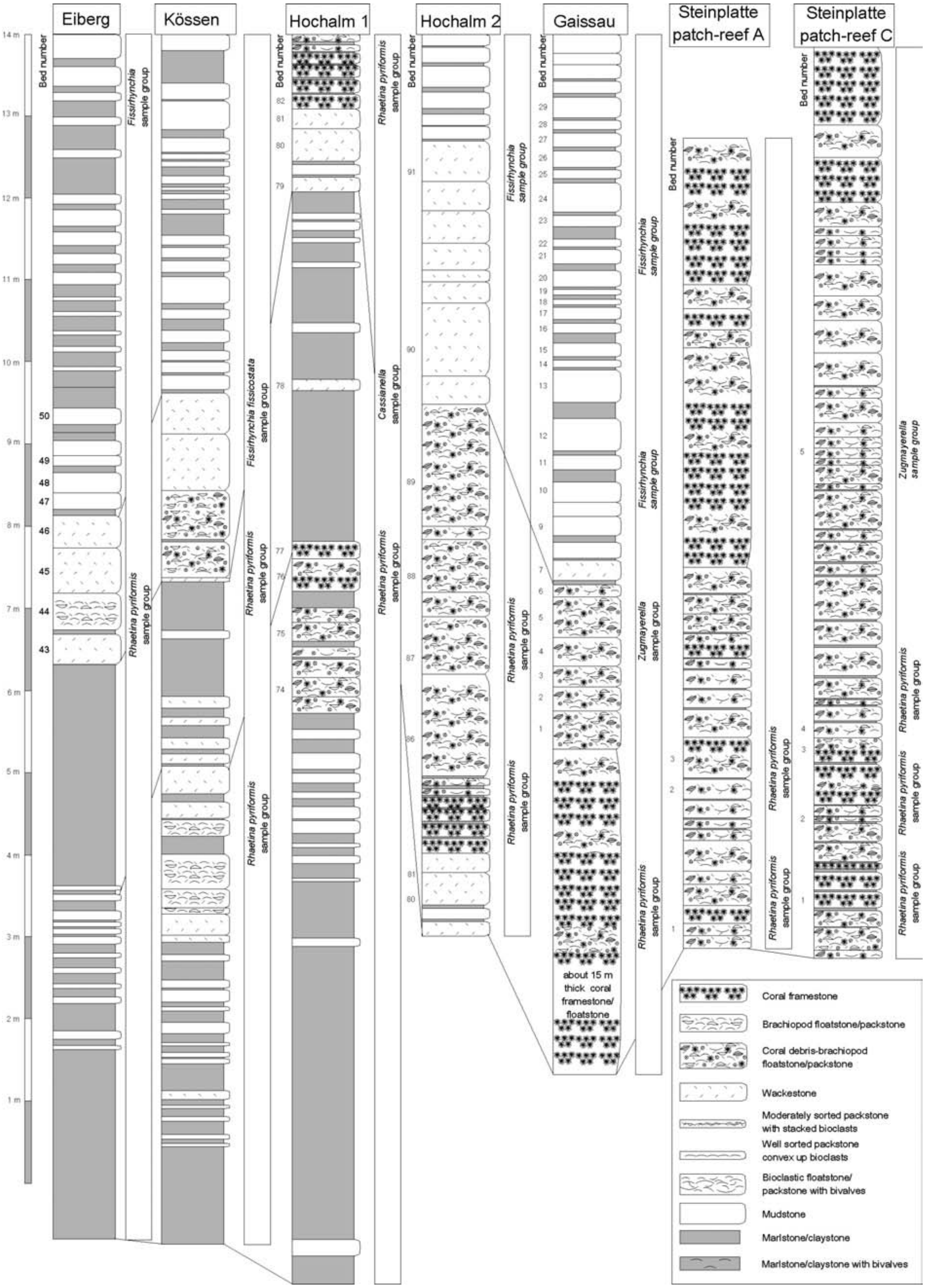


Figure 10 - Stratigraphic distribution of sample groups in the upper parts of the Hochalm Member and the lowermost part of the Eiberg Member. The six sections show a lateral transition from basinal environments (Eiberg, Kössen, Hochalm and Gaissau) into patch-reefs at Steinplatte (see correlation lines).

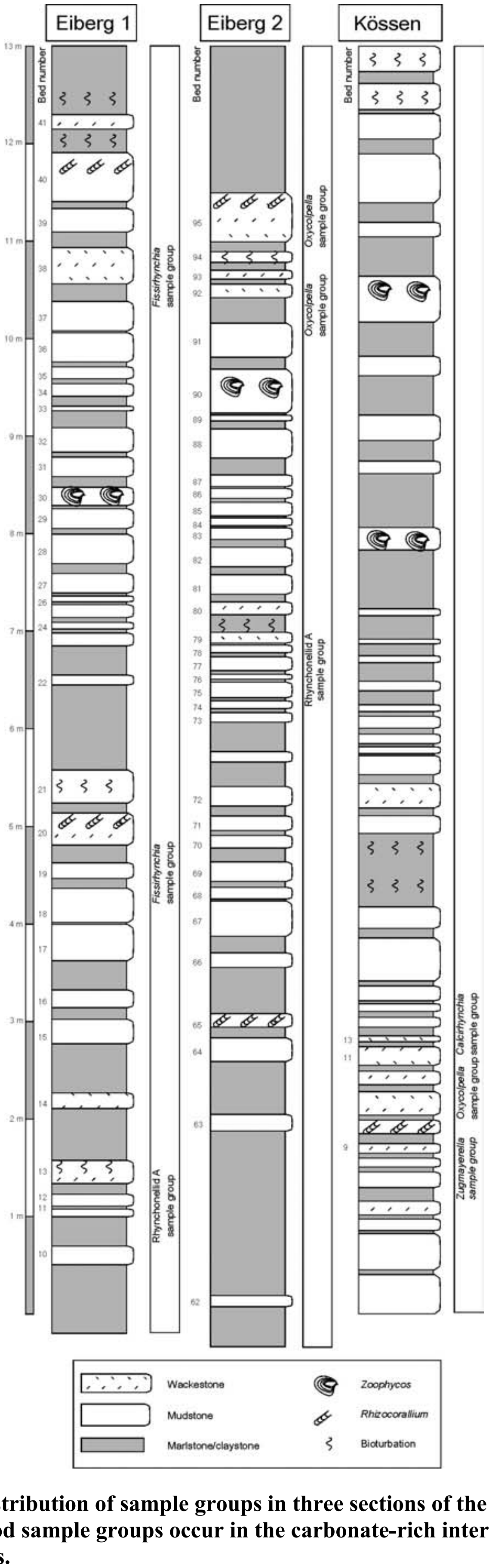


Figure 11 - Stratigraphic distribution of sample groups in three sections of the middle part of the Eiberg Member (Unit 6). Brachiopod sample groups occur in the carbonate-rich intervals characterized by dominance of limestone beds.

Community variation along a temporal gradient

There are significant differences in species composition between the stratigraphic units (ANOSIM, Table 1). All six pairwise comparisons between units 2, 3, 4 and 5-8 are significant at $p<0.0001$, indicating substantial community turnover during the deposition of the Kössen Formation (Table 1). Therefore, in order to decrease compositional heterogeneity, the environmental distribution of benthic fauna is analyzed below separately for Unit 2, Unit 3 and units 4-8. In addition, there are significant differences in species composition between the siliciclastic and carbonate intervals in Unit 2 ($R = 0.49$, $p < 0.0001$, Table 1). The carbonate intervals are dominated by brachiopods and some epifaunal bivalves (*R. gregaria* sample group), in contrast to the siliciclastic intervals dominated by infaunal (*Isocyprina* sample group) and semi-infaunal bivalves (*Gervillaria* sample group, Fig. 8). Epifaunal bivalves occur also in the siliciclastic intervals but are uncommon. Although the differences in species composition between the siliciclastic and carbonate intervals in Unit 3 are insignificant ($p = 0.69$, Table 1), some bivalve groups are typical of the siliciclastic intervals only (i.e., *Gervillaria*, *Cassianella*, and *Chlamys* sample groups, Fig. 9). In addition, the *R. pyriformis* sample group occurs in the carbonate intervals only, thus also indicating compositional differences between the carbonate and siliciclastic deposits (Fig. 9). The uppermost part of the Hochalm Member (Fig. 10) is represented by coral framestones and floatstones with brachiopod sample groups (*R. pyriformis* and *Zugmayerella* sample groups). Several sample groups with brachiopods (*Zugmayerella, Fissirhynchia, Oxycolpella*, *Calcirhynchia*, and Rhynchonellid sp. A) occur in bioturbated mudstones and marlstones in the carbonate intervals of the Eiberg Member (Fig. 11). The siliciclastic intervals of the Eiberg Member are almost devoid of shelly benthos.

	R Statistic	P-value	Permutations	Number of permuted R≥observed R
Global test	0.525	<0.0001	10000	0
Pairwise tests:				
Unit 2 vs. Unit 3	0.292	<0.0001	10000	0
Unit 2 vs. Unit 4	0.54	<0.0001	10000	0
Unit 2 vs. Unit 5-8	0.764	<0.0001	10000	0
Unit 3 vs. Unit 4	0.592	<0.0001	10000	0
Unit 3 vs. Unit 5-8	0.769	<0.0001	10000	0
Unit 4 vs. Unit 5-8	0.507	<0.0001	10000	0
Unit 2 - siliciclastic vs. carbonate interval	0.492	0.0001	10000	1
Unit 3 - siliciclastic vs. carbonate interval	-0.04	0.69	10000	6896

Table 1 - Results of ANOSIM, which tests differences in species composition among the four stratigraphic units. The Bonferroni correction lowers the alpha value in pairwise tests to 0.0083 (0.05/6).

Community variation along an onshore-offshore gradient

In this part, compositional variation of the sample groups and differences in species and guild composition between the depth habitats are analyzed with NMDS. In addition, ANOSIM were employed to test for differences in composition between habitats. This is performed separately for Unit 2, Unit 3 and units 4-8. The onshore-offshore gradient is interpreted separately for the siliciclastic and carbonate intervals.

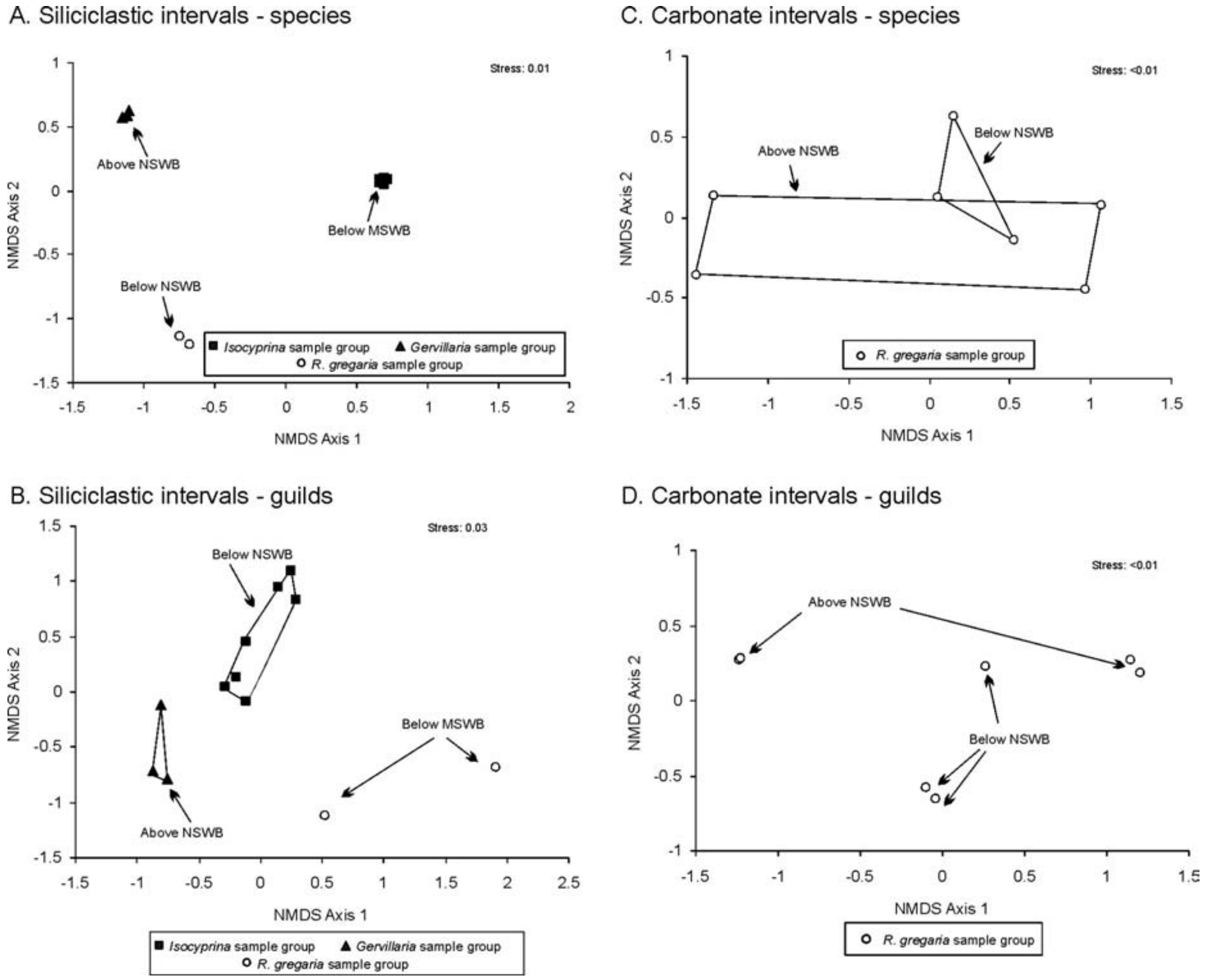


Figure 12 - Ordination of samples of Unit 2 showing between-habitat differences in species and guild composition. (A) Siliciclastic intervals - Q-mode NMDS based on species composition. (B) Siliciclastic intervals - Q-mode NMDS based on guild composition. (C) Carbonate intervals - Q-mode NMDS based on species composition. (D) Carbonate intervals - Q-mode NMDS based on guild composition.

Onshore-offshore gradient of Unit 2

Siliciclastic intervals: ANOSIM shows that there are significant differences (R=1, p<0.00012, Table 2) in species composition among three depth habitats from the siliciclastic intervals. The between-habitat differences are also visible in NMDS (Fig. 12A). Similarly, compositional segregation for three depth habitats follows from the guild composition (Table 2, Fig. 12B). The habitats above NSWB, represented by hummocky-cross stratified deposits and floatstones with stacked valves in the middle parts of the siliciclastic intervals, are dominated by the endobyssate *Gervillaria* (Fig. 13). The habitats below NSWB, associated with deposits exhibiting planar or wavy mm-scale stratification in the lower parts of the siliciclastic intervals, are dominated by shallow infaunal eulamellibranch bivalves (*Isocyprina* sample group). Although the two samples dominated by pedunculate brachiopods (*R. gregaria* sample group) occur in single-event packstones similarly as the *Isocyprina* sample group, they are embedded between non-laminated marlstones or mudstones, indicating little storm disturbance. Therefore, these samples are assigned to the most distal part of the onshore-offshore gradient, close to MSWB (Fig. 13).

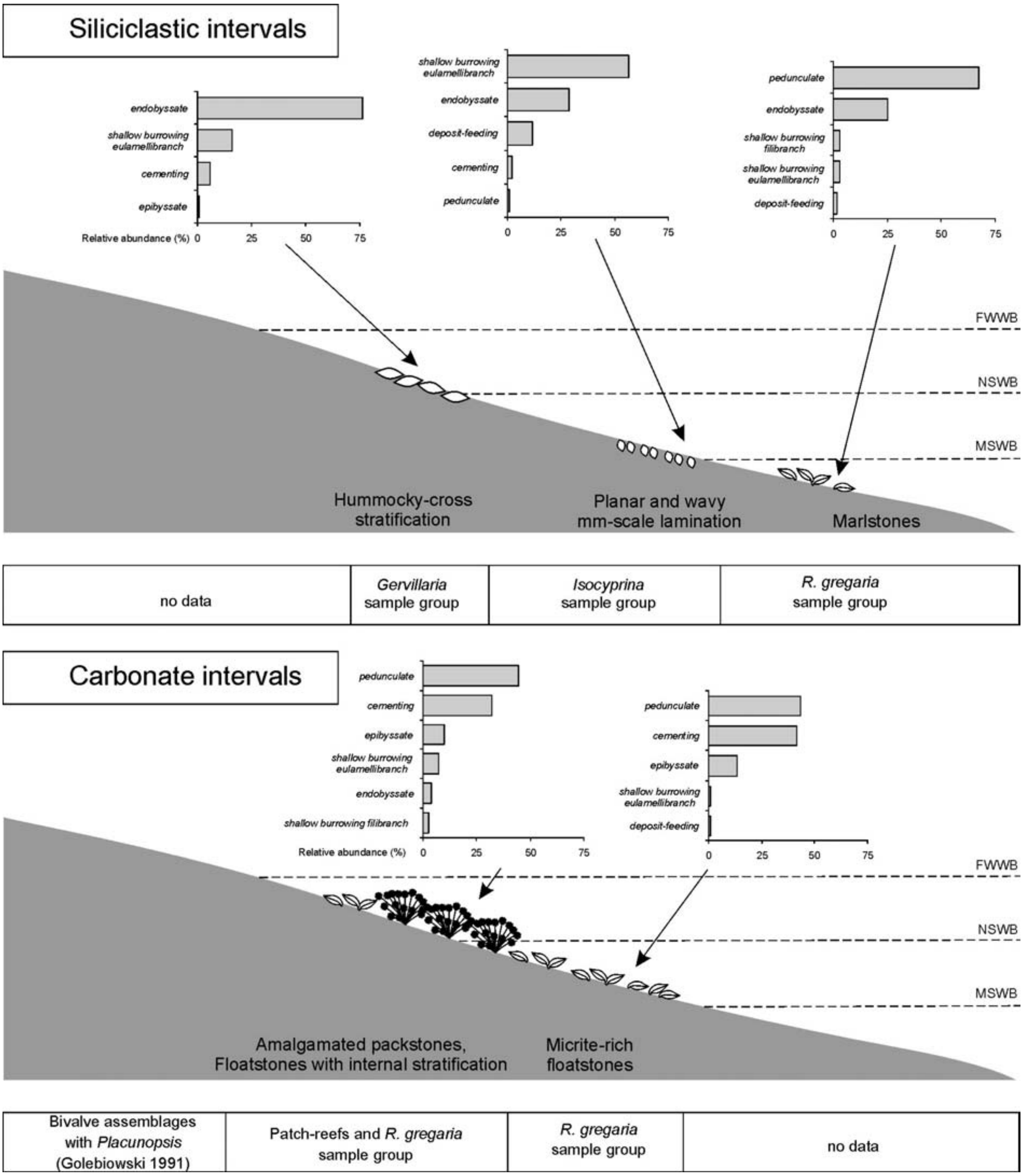


Figure 13 - Distribution of sample groups along an onshore-offshore gradient in Unit 2. A. Siliciclastic intervals. Note that bivalves dominate in shallow habitats and brachiopods in deep habitats. B. Carbonate intervals. Note that brachiopods dominate in shallow habitats above NSWB.

Carbonate intervals: Because the number of samples from the carbonate intervals is very low, the p-values are inconclusive (Table 2, Fig. 12C, D). In the onshore-offshore gradient, the habitats above NSWB are represented by bioclastic packstones and coral floatstones with internal storm stratification, and the habitats below NSWB by micrite-rich bioturbated floatstones (Fig. 13). In one case, a brachiopod floatstone with signs of storm-reworking passes upward into well sorted and densely packed packstones and rudstones, suggesting that brachiopods lived close to FWWB. In addition to the *R. gregaria* sample group, coral deposits represent relics of coral carpets or initial patch-reefs typical of habitats above NSWB. An environmental trend related to increasing turbidity and sedimentation rate may have caused separation of corals and level-bottom fauna because corals decline in abundance with an increase in marl content. A further ecologic zone in onshore direction may have been dominated by bivalve *Placunopsis alpina* or by megalodonts because the carbonate intervals are replaced in landward direction by deposits that represent restricted carbonate lagoons and tidal flats (Golebiowski, 1991).

	R Statistic	P-value	Permutations	Number of permuted R≥observed R
Unit 2-carbonate interval-species				
Above NSWB vs. below NSWB	0.056	(0.34)	35	12
Unit 2-carbonate intervals-guilds				
Above NSWB vs. below NSWB	0.093	(0.37)	35	13
Unit 2-siliciclastic interval -species				
Global test	1	<0.00012	7920	0
Within-group comparisons:				
Above NSWB vs. below NSWB	1	(0.028)	36	1
Above NSWB vs. below MSWB	1	0.0083	120	1
Below NSWB vs. below MSWB	1	(0.1)	10	1
Unit 2-siliciclastic intervals- guilds				
Global test	0.83	<0.00012	7920	0
Within-unit comparisons:				
Above NSWB vs. below NSWB	0.981	(0.028)	36	1
Abobe NSWB vs. below MSWB	0.722	0.0083	120	1
Below NSWB vs. below MSWB	0.917	(0.1)	10	1

Table 2 - Results of ANOSIM, which tests differences in species and guild composition in different bathymetric settings of Unit 2. The tests are performed separately for the carbonate and siliciclastic intervals. The Bonferroni correction lowers the alpha value in pairwise tests to 0.017 (0.05/3). The p-values in parentheses are inconclusive due to low number of permutations.

Onshore-offshore gradient of Unit 3

Siliciclastic intervals: ANOSIM shows that there are significant differences in species (R=0.706, p<0.0001) and guild composition (R=0.641, p<0.0001) among three depth habitats (Fig. 14A, B). The pairwise differences in species and guild composition between the particular depths are always of high or borderline significance (Table 3). The habitats above NSWB are dominated by the endobyssate *Gervillaria* occurring in thin shell beds and pavements in beds with hummocky-cross stratification (Fig. 15). The shallow burrowing *Myophoriopis* is typical of the habitats below NSWB (Fig. 15). Epibyssate and cementing bivalves are also common in the habitats below NSWB. The *Cassianella* and *Chlamys* sample groups dominated by epifaunal bivalves occur typically in marlstones and mudstones below MSWB. The soft-bottom, siliciclastic-rich habitats below MSWB are thus dominated by epibyssate and free-lying filibranchs (Fig. 15).

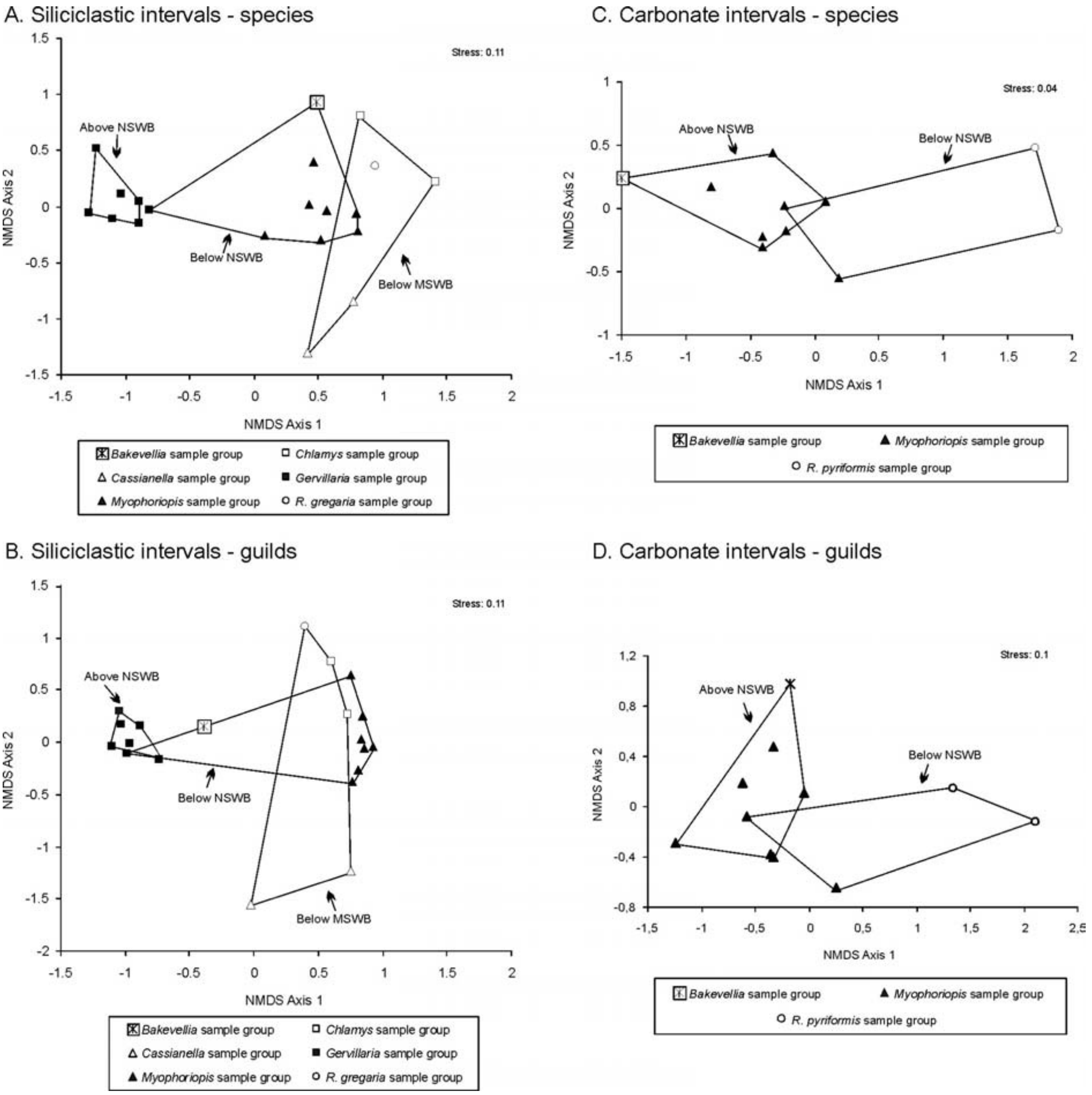


Figure 14 - Ordination of samples of Unit 3 showing between-habitat differences in species and guild composition. (A) Siliciclastic intervals - Q-mode NMDS based on species composition. (B) Siliciclastic intervals - Q-mode NMDS based on guild composition. (C) Carbonate intervals - Q-mode NMDS based on species composition. (D) Carbonate intervals - Q-mode NMDS based on guild composition.

Carbonate intervals: NMDS shows only partial compositional overlap between the habitats below and above NSWB (Fig. 14C, D). ANOSIM shows the difference based on species (R=0.407, p=0.036) and guild composition (R=0.365, p=0.052) is of borderline significance (Table 3). The habitats above NSWB are dominated by shallow burrowing eulamellibranchs and epibyssate, endobyssate and cementing guilds. The habitats below NSWB are either dominated by shallow burrowing eulamellibranchs, or by pedunculate brachiopods. However, the *Rhaetina pyriformis* sample group dominated by pedunculates and epifaunal bivalves is limited to the habitats below NSWB. The beds with *R. pyriformis* lack complex internal stratification which would point to episodic storm events, in contrast to the beds with *Myophoriopis* and *Bakevellia*. Although fragmentation and disarticulation may reach relatively high levels in floatstones with *R. pyriformis*, high proportions of borers and microborers point to biogenic destruction. In addition, limestone beds with *Myophoriopis* and *Bakevellia* are mostly thin and alternate with thin marlstones, indicating a higher siliciclastic supply and a lower rate of carbonate production, in contrast to thicker beds with coral debris and brachiopods. The co-existence of bivalve and brachiopod communities along one bathymetric transect is indicated by the presence of the *Myophoriopis* sample group in Eiberg and the *R. pyriformis* sample group in Gaissau and Hochalm at comparable stratigraphic levels (Fig. 9). Therefore, communities dominated by infaunal guilds were living closer to the siliciclastic source, in habitats with a higher sedimentation rate and higher storm-reworking. Brachiopods, epifaunal bivalves and less common shallow infaunal eulamellibranchs populated more distal and deeper habitats with reduced sediment supply (Fig. 15).

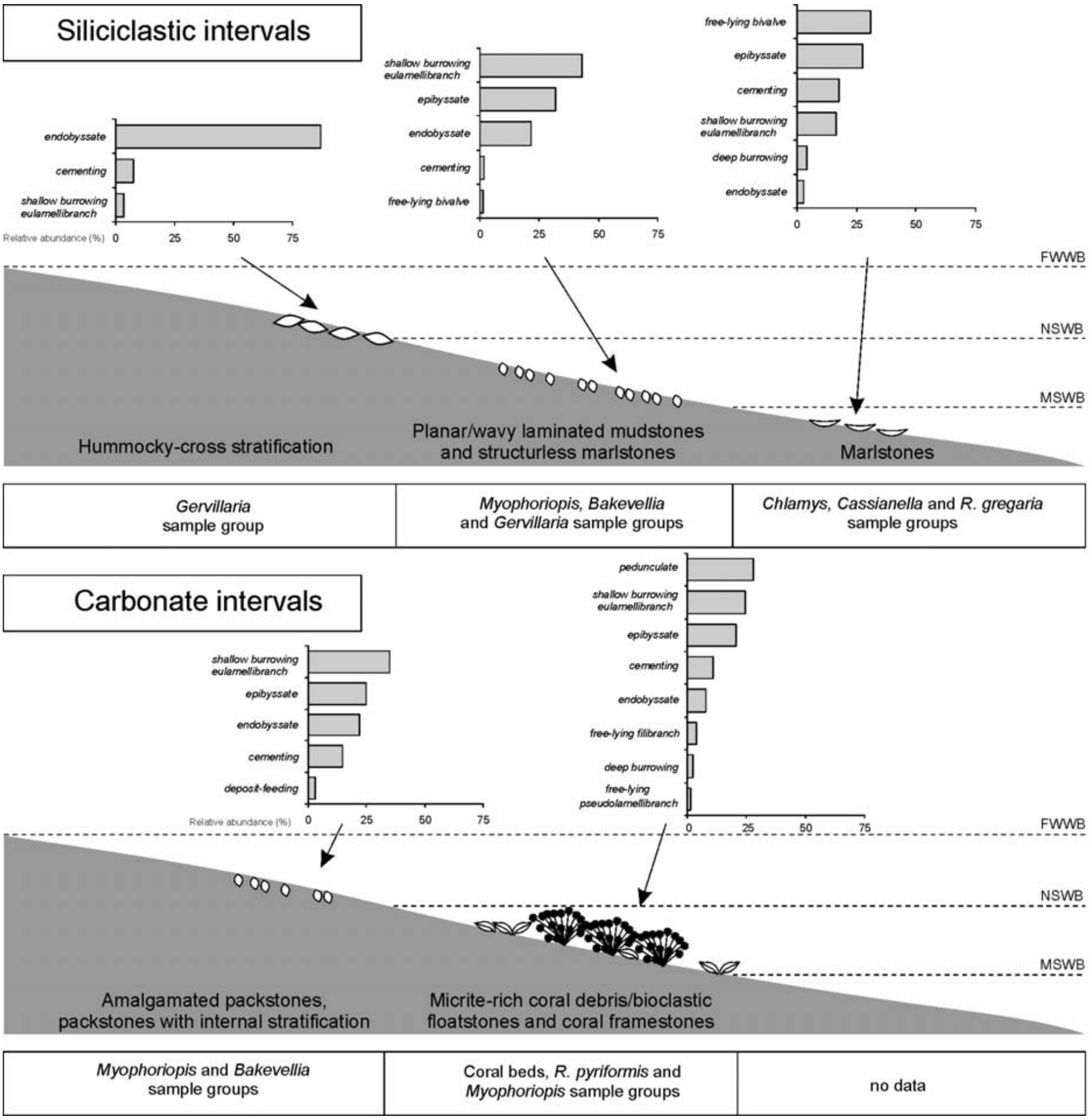


Figure 15 - Distribution of sample groups along an onshore-offshore gradient in Unit 3. (A) Siliciclastic intervals. Note that free-lying bivalves are abundant in deep habitats below MSWB. (B) Carbonate intervals. Note that bivalves dominate in shallow habitats and brachiopods in deep habitats.

	R Statistic	P-value	Permutations	Number of permuted R≥observed R
Unit 3-carbonate interval-species				
Above NSWB vs. below NSWB	0.407	0.036	330	12
Unit 3-carbonate intervals-guilds				
Above NSWB vs. below NSWB	0.341	0.061	330	20
Unit 3-siliciclastic interval -species				
Global test	0.706	<0.0001	10000	0
Within-group comparisons:				
Above NSWB vs. below NSWB	0.762	0.0004	10000	4
Above NSWB vs. below MSWB	0.934	0.001	792	1
Below NSWB vs. below MSWB	0.321	0.022	2002	45
Unit 3-siliciclastic intervals- guilds				
Global test	0.641	<0.0001	10000	0
Within-unit comparisons:				
Above NSWB vs. below NSWB	0.694	0.0008	10000	8
Abobe NSWB vs. below MSWB	0.854	0.0012	792	1
Below NSWB vs. below MSWB	0.3	0.028	2002	57

Table 3 - Results of ANOSIM, which tests differences in species and guild composition in different bathymetric settings of Unit 3. The tests are performed separately for the carbonate and siliciclastic intervals. The Bonferroni correction lowers the alpha value in pairwise tests to 0.017 (0.05/3).

Onshore-offshore gradient of units 4-8

Siliciclastic intervals: No quantitative samples are available from the siliciclastic-rich intervals of the Eiberg Member, which are mostly completely devoid of shelly benthic fauna. Golebiowski (1989) detected rare finds of epifaunal bivalves (*Oxytoma*) and brachiopods (rhynchonellids and *Oxycolpella*) that are equivalent to the species known from the carbonate intervals of the Eiberg Member. Most of the beds in the siliciclastic intervals do not show any trace fossils and fine cm-scale alternation of mudstones and marlstones indicate restricted levels of bioturbation. Some beds contain very common ammonites. The rarity of shelly benthos is most probably a real consequence of low population density due to unfavorable bottom conditions.

Carbonate intervals: Six brachiopod sample groups occur in the upper parts of the Hochalm Member (Unit 4) and in the carbonate-rich intervals of the Eiberg Member (units 5-8). All samples from this stratigraphic part of the Kössen Formation are dominated by brachiopods. NMDS (Fig. 16A, B) and ANOSIM show significant differences in species (R=0.336, p=0.0012, Table 4) and guild composition (R = 0.524, p = 0.0001, Table 4) in the habitats above and below MSWB. Communities dominated by pedunculate brachiopods are common in coral patch-reefs and coral beds representing hard-bottom and mixed-bottom habitats above and below NSWB (Fig. 17). In addition to the dominant pedunculate brachiopods, coral patch-reefs at Steinplatte were colonized by epibyssate, endobyssate, and cementing bivalves. The soft-bottom habitats below MSWB were dominated either by pedunculate brachiopods (*Fissirhynchia)* or free-lying brachiopods (Fig. 17; *Oxycolpella* and rhynchonellids). The deposits below MSWB are bioturbated and show no signs of high-energy disturbance. The higher proportion of free-lying brachiopods towards soft-bottom habitats below

MSWB may reflect decreased ability of pedunculate brachiopods to cope with soft-bottom conditions and/or decreased ability of free-lying brachiopods to compete for food or space in hard- or mixed-bottom habitats. The absence or rarity of infaunal or semi-infaunal bivalves is noteworthy.

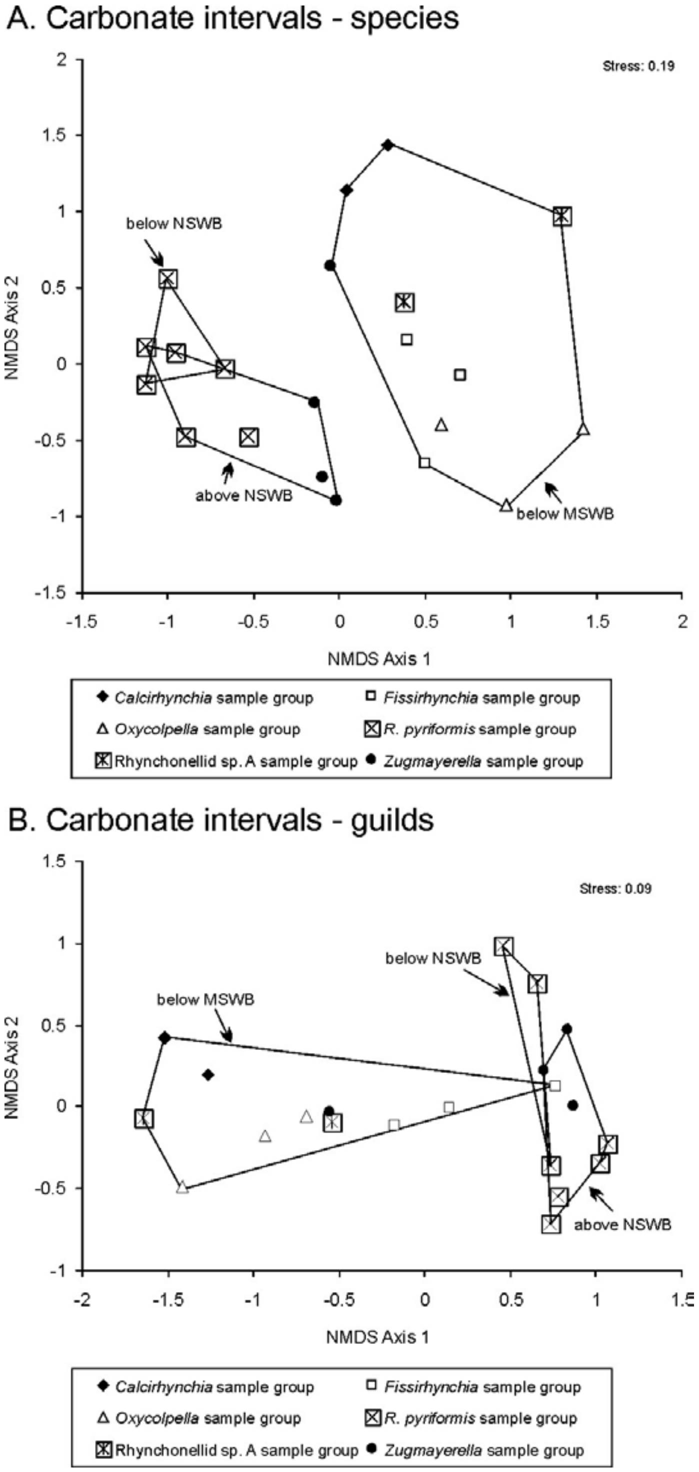


Figure 16 - Ordination of samples of Unit 4 and Eiberg Member showing between-habitat differences in species and guild composition. (A) Q-mode NMDS based on species composition. (B) Q-mode NMDS based on guild composition.

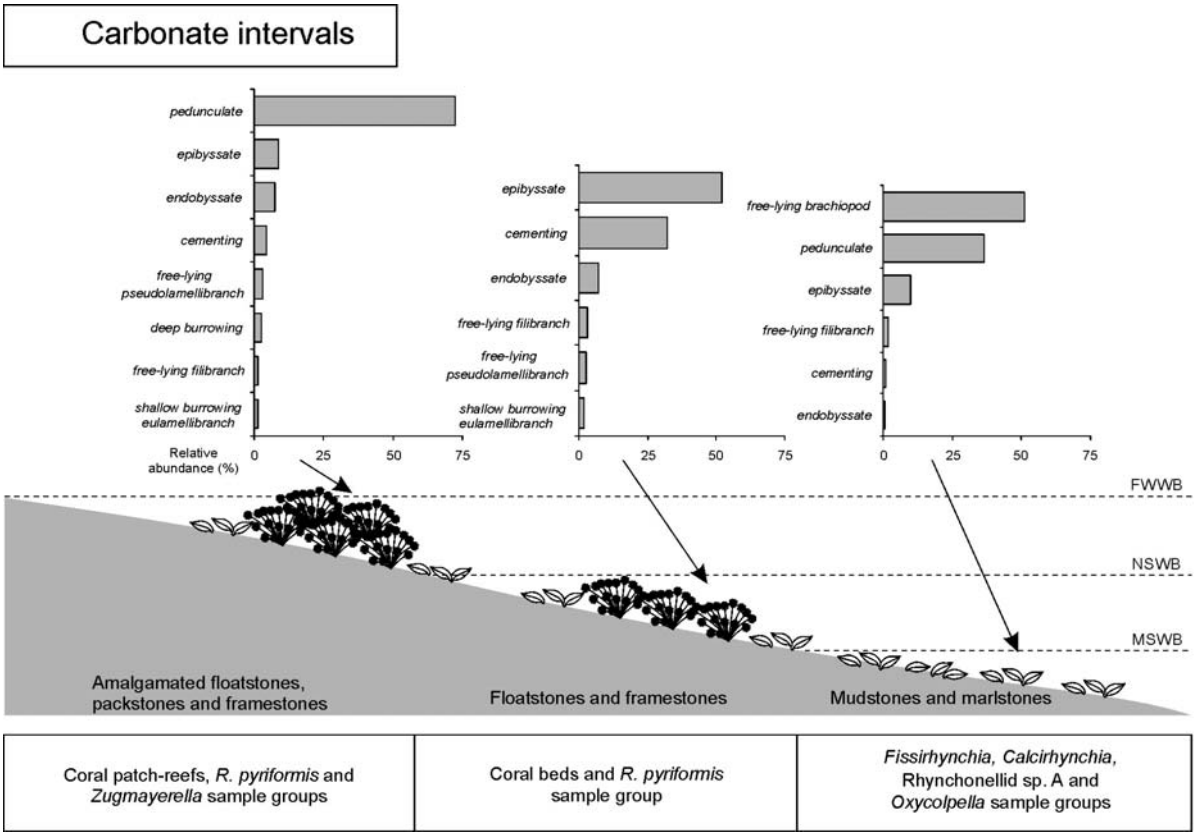


Figure 17 - Distribution of sample groups along an onshore-offshore gradient in Unit 4 and in the carbonate intervals of the Eiberg Member. Note the absence of infaunal bivalves.

Unit 4-8 - species	R Statistic	P-value	Permutations	Number of permuted R≥observed R
Global test	0.336	0.0012	10000	12
Pairwise tests:				
below NSWB, below MSWB	0.467	0.003	364	1
below NSWB, above NSWB	0.115	0.27	120	33
below MSWB, above NSWB	0.384	0.0004	10000	4
Unit 4-8 - guilds				
Global test	0.558	0.0001	10000	1
Pairwise tests:				
below NSWB, below MSWB	0.552	0.008	364	3
below NSWB, above NSWB	0.341	0.075	120	9
below MSWB, above NSWB	0.639	<0.0001	10000	4

Table 4 - Results of ANOSIM, which tests differences in species and guild composition in different bathymetric settings of Unit 4 and in the Eiberg Member. The Bonferroni correction lowers the alpha value in pairwise tests to 0.017 (0.05/3).

Discussion

Three patterns emerge from the compositional variation and onshore-offshore distribution of species and guilds. First, exploring the patterns in Q-mode and R-mode analyses, brachiopod guilds co-existed more commonly with epifaunal bivalves *than* with infaunal and semi-infaunal bivalves. Note that the reverse is not necessarily true because epifaunal bivalve guilds can commonly co-occur both with brachiopods and infaunal and semi-infaunal bivalves. Second, the communities dominated by brachiopods and epifaunal bivalves were abundant in some soft-bottom habitats, both in the lower and upper part of the Kössen Formation. This dominance in soft-bottom habitats is more typical of Paleozoic than of present-day habitats. Third, brachiopod-dominated communities expanded in their depth distribution as the siliciclastic regime was repeatedly replaced by the carbonate regime during the deposition of the lower part of the Kössen Formation.

Co-existence of brachiopods with epifaunal filibranchs

As follows from Q-mode and R-mode analyses, (1) brachiopods as a group were characterized by distinct distribution pattern (i.e., brachiopod sample groups do not overlap with bivalve sample groups, and brachiopod species co-exist more commonly with other brachiopods than with bivalves), and (2) brachiopod guilds co-existed more commonly with epifaunal than with infaunal and semi-infaunal bivalves. The similar compositional separation between brachiopods and bivalves was observed in the Pennsylvania-Permian deposits by Olszewski and Patzkowsky (2001).

The distinct distribution patterns of epifaunal and infaunal/semi-infaunal guilds are supposed to reflect differences in substrate stability and consistency (Rhoads, 1974; Woodin, 1976; Thayer, 1983; Snelgrove and Butman, 1994). In general, as rhynchonelliformean brachiopods are epifaunal, substrate properties are supposed to be the main factors that govern their abundance (Fürsich, 1976; Thayer, 1983; Fürsich et al., 1991; Aberhan, 1992, 1994). However, in addition to their similar response to variations in substrate quality, epifaunal bivalves and brachiopods may share also other environmental preferences, mainly related to variations in nutrient supply, turbidity and oxygen levels. Along the onshore-offshore gradient in the Kössen Basin, brachiopods and some epifaunal bivalves consistently dominate in the habitats that are affected by lower siliciclastic and nutrient supply than the habitats dominated by infaunal and semi-infaunal bivalves. This indicates that their distribution correlates with variations in land-derived nutrient supply and turbidity. Note that epifaunal bivalves of the Kössen Formation are less restricted in distribution than brachiopods, i.e., they can also occupy habitats dominated by infaunal and semi-infaunal bivalves.

Epifaunal bivalves and brachiopods may respond in a similar way to low nutrient supply, in contrast to infaunal suspension-feeding bivalves. Although there is high variation in clearance rates even on the intraspecific level and clearance and rejection rates vary with turbidity levels (Iglesias et al., 1996; Urrutia et al., 1997; Hawkins et al., 1998, 2001; Navarro et al., 2003), it seems that filibranch and pseudolamellibranch bivalves, which are typically epifaunal, have usually higher clearance rates under low particle concentrations and are thus more efficient under reduced nutrient supply than infaunal, mostly eulamellibranch bivalves (Bacon et al., 1998; Velasco and Navarro, 2002). This difference can be related to the higher ctenidial surface or better retention efficiency of filibranch and pseudolamellibranch gills. The metabolic demands of infaunal bivalves thus may not be fulfilled under nutrient-poor conditions, in contrast to filibranch and pseudolamellibranch bivalves. Bathymetric trends in bivalve diversity seem to be in accord with this hypothesis about differential nutrient supply requirements. Hickman (1984) observed that diversity of heterodonts markedly decreases towards bathyal and abyssal habitats, in contrast to pteriomorph bivalves.

The clearance rates are lower in brachiopods than in filibranch bivalves (Rhodes and Thompson, 1992, 1993) but brachiopods can cope with nutrient-poor conditions due to their mechanisms that minimize energetic expenditure, such as low metabolic rates, laminar flow in active pumping and ability to exploit ambient water currents (LaBarbera, 1977, 1981b; Curry et al., 1989; Peck et al., 1989, 2005; Peck, 1996). Brachiopods can thus have similar preferences as filibranch bivalves with respect to the nutrient supply regime, although both differ in their adaptive strategies (i.e., bivalves have higher clearance rates and brachiopods lower metabolic demands). It should be noted that modern infaunal protobranchs are able to live in habitats with extreme variations in nutrient supply (Crame, 2002). However, deposit-feeding nuculids are represented by one rare species in the Kössen Formation so they do not contribute to the differential distribution of epifauna and infauna.

Furthermore, the algal concentrations at which clearance rates decrease or feeding stops are lower in brachiopods than in bivalves (Rhodes and Thompson, 1993). Terebratulid brachiopods stop their feeding at algal concentrations higher than 5,000 cells/ml and rhynchonellid brachiopods decrease their clearance rates in concentrations of 10,000 cells/ml. In contrast, the feeding rates of bivalves start to decrease at concentrations which are usually much higher than 10,000 cells/ml (Rhodes and Thompson, 1993). This indicates that rhynchonelliformean brachiopods are more vulnerable to habitats with high particle concentrations than bivalves. Thayer (1986) showed that brachiopods possess various pre-ingestion mechanisms which allow coping with high turbidity conditions, and some brachiopods live in highly turbid conditions (Tunnicliffe and Wilson, 1988). However, the difference in the threshold concentrations indicates that this ability is probably lower in brachiopods *than* in bivalves. Epifaunal bivalves with heterorhabdic filibranch or pseudolamellibranch gill have a high selection capacity, enabling them to live in highly turbid environments (Cognie et al., 2003; Beninger et al., 2004).

Although the differential feeding ability between bivalves with different gill type, and between bivalves and brachiopods, is still not clearly resolved, it is used here as a working hypothesis that can be tested via comparison of communities from habitats with distinct nutrient supply and turbidity. Note that relatively high clearance rates of filibranch bivalves and low metabolic demands of brachiopods indicate that both can potentially better cope with low oxygen concentrations than eulamellibranch bivalves with lower clearance rates/higher metabolic demands (Childress and Seibel, 1998; Levin, 2003). Brachiopods and filibranch bivalves can thus also co-occur due to their similar response with respect to oxygen fluctuations.

Dominance of brachiopods and epifaunal bivalves in soft-bottom habitats

Several hypotheses were proposed in order to explain the absence or rarity of epifaunal, immobile suspension-feeders in present-day soft-bottom habitats, which contrasts with Paleozoic and Mesozoic times when soft-bottom habitats were commonly dominated by poorly mobile epifaunal suspension-feeders (Thayer, 1983; Jablonski and Bottjer, 1983; Holland and Patzkowsky, 2004). In general, it is supposed that a combination of increased biotically-induced sediment disturbance and increased predation during the Mesozoic led to a change in ecology of soft-bottom habitats and decline of immobile epifaunal suspension-feeders (Vermeij, 1977; LaBarbera, 1981a; Thayer, 1979, 1983; Harper and Skelton, 1993; Ozanne and Harries, 2002; Lockwood, 2004; Kosnik, 2005).

In a quantitative survey of bivalve and brachiopod guilds, Thayer (1983) regarded the free-lying and endobyssate bivalves and free-lying brachiopods as those guilds, which are vulnerable to higher sediment-mediated disturbance in soft-bottom habitats. Although cementing and epibyssate bivalves and pedunculate brachiopods are also poorly mobile, they were not included by Thayer into the category which is vulnerable to sediment-mediated disturbance. This was because they were supposed to be mainly inhabitants of hard-bottom habitats. However, these guilds commonly occupy also mixed-bottom or soft-bottom habitats with a possibility for attachment to isolated hard substrates. The increase in sediment-disturbance in such habitats will also be disadvantageous for these guilds. Therefore, in this paper, all poorly mobile epifauna, including also pedunculate brachiopods, are assumed to have been potential victims of high sediment disturbance.

Below, multiple hypotheses explaining the absence of infaunal suspension-feeding bivalves in soft-bottom habitats are evaluated. As infaunal suspension-feeding bivalves are locally very common in the Kössen Formation, their rarity or absence in soft-bottom habitats should be related to some taphonomic or ecologic explanation. Three soft-bottom habitats dominated by epifaunal suspension-feeders will be evaluated, including micrite-rich habitats of the carbonate intervals of the Hochalm Member, mudstones and marlstones of the lower parts of the siliciclastic intervals of the Hochalm Member, and mudstones and marlstones of the carbonate intervals of the Eiberg Member. It is important to note that in soft-bottom habitats there can be still enough sites for attachment of juvenile brachiopods or bivalves (e.g., shell debris and soft-bodied benthic animals that can also provide stable support for attachment). Some brachiopods in the Eiberg Member commonly show clumpy distribution on bedding planes, indicating that they formed clusters comparable to benthic islands (Zuschin et al., 1999).

(1) Taphonomic bias due preferential destruction of aragonitic bivalves. Higher susceptibility of aragonite to dissolution can cause that infaunal bivalves will be underrepresented with respect to their community-level abundance because brachiopods and most of epifaunal bivalves are mainly calcitic and infaunal bivalves mainly aragonitic (Jablonski and Bottjer, 1983). This preservation bias can be enhanced by a sampling bias against aragonitic bivalves because moulds are more difficult to extract from lithified rocks than calcitic shells. In the Hochalm Member, samples dominated by brachiopods or epifaunal bivalves contain originally aragonitic bivalves that are mostly preserved as recrystallized shells in marlstones and micrite-rich floatstones of the carbonate and siliciclastic intervals. Internal moulds or incompletely dissolved shells are locally visible but do not prevail in comparison to unaltered shells in thin-sections. In addition, marlstones dominated by infaunal and semi-infaunal bivalves are lithologically comparable to marlstones with brachiopods and epifaunal bivalves, indicating that the taphonomic biases alone do not explain the compositional difference. In the Eiberg Member, aragonitic bivalves are rare or absent in the carbonate intervals. However, well-preserved ammonite shells occur both in the Eiberg Member. Importantly, signs of dissolution comparable to those observed in the Hochalm Member were not observed in thin-sections from the Eiberg Member. Low abundance of aragonitic bivalves thus probably still reflects the original community composition and is not a preservation artifact.

(2) Inhibited burrowing ability and enhanced substrate stability. Firm or shell-rich substrate inhibits penetration by infauna or leads to a decrease in growth rates of infauna, with higher vulnerability to predation or competition as the by-product (Kidwell and Jablonski, 1983; Oschmann, 1988; Aberhan, 1992). Enhanced substrate stability may be related to high production rates of epifaunal organisms (Woodin, 1976), to reduced sedimentation rates, or to taphonomic feedback (Kidwell and Jablonski, 1983). Although the results of these processes do not fit into the category of soft-bottom habitats, the difference between soft and firm bottom is not always unequivocal in the fossil record. *Thalassinoides*-like burrows co-occurring with *R. gregaria* in the carbonate intervals of the Hochalm Member do not show scratch marks, indicating soft-bottom conditions. In the Eiberg

Member, brachiopods and epifaunal bivalves dominate in shell-poor mudstones and marlstones that contain *Zoophycos* and *Rhizocorallium*. *Rhizocorallium* burrows are filled with meniscate backfills formed by alternation of pellets and marl. In addition, shells and fragments in thin-sections show highly irregular, commonly clumped distribution, indicative of bioturbation and soft-bottom conditions.

(3) Inhibited recruitment of infaunal bivalves due to soupy substrate. This hypothesis was suggested by Jablonski and Bottjer (1983) to explain the absence or rarity of infaunal suspension-feeders in the Upper Cretaceous Chalk communities. Higher survival of epifaunal larvae in soft, unstable substrates contrasts with inhibited recruitment of larvae of infaunal suspension-feeders. As they argued, larvae of infaunal suspension-feeders which settle directly onto the soupy sediment-water interface may suffer higher mortality due to swamping, clogging of respiratory organs, and ingestion by deposit-feeders, in contrast to larvae of epifaunal organisms, which attach to hard substrata. In addition, those infaunal individuals that survive larval settlement are unable to maintain position and function efficiently in unstable carbonate mud. In contrast, larvae of epifaunal suspension-feeders settle onto hard substrata and can thus avoid such problems. As complex feeding and dwelling trace fossils co-occur with brachiopods and epifaunal bivalves in the carbonate intervals of the Hochalm and Eiberg Member, this hypothesis can be excluded. Marlstones in the siliciclastic intervals of the Hochalm Member do not show any recognizable trace fossils and the conditions with unstable substrate can be possible for samples dominated by the reclining bivalve *Cassianella*. This bivalve could maintain stable orientation on the sediment-water interface due its iceberg strategy (Thayer, 1975).

(4) Inhibited recruitment of infaunal bivalves due to hypoxia. Dominance of epifaunal suspension-feeders in soft-bottom habitats is also explained by anoxic conditions below or at the sediment-water interface, excluding deep and possibly also shallow infaunal mollusks (Oschmann, 1988; Aberhan, 1992). In addition, epifaunal bivalves with high clearance rates and brachiopods with low metabolic demands can be able to cope with oxygen-deficient conditions. The typical epifaunal guilds of the Mesozoic oxygen-controlled communities were represented by free-lying, flat-valved suspension-feeding bivalves, deposit-feeding nuculids and, since the Late Jurassic, shallow burrowing bivalves (Aberhan, 1994). Oxygen-controlled Rhaetian communities could be atypical because typical Late Triassic flat clams (*Monotis, Daonella, Halobia*) were extinct already before Rhaetian times. In contrast, Early Jurassic taxa such as *Bositra, Entolium* or *Gryphaea* were rare or absent during Rhaetian.

Bioturbated, micrite-rich deposits in the carbonate intervals of the Hochalm Member cannot be explained by this hypothesis. Similarly, abundance of brachiopods and epifaunal bivalves is linked to bioturbated beds with abundant trace fossils in the carbonate intervals of the Eiberg Member. Abundant crinoid ossicles and shell debris commonly encrusted by serpulids and foraminifers also indicate that bottom waters were well oxygenated. However, assemblages from the siliciclastic intervals of the Hochalm Member can be in accord with this hypothesis. A decrease in oxygen concentrations is indicated by high proportions of well preserved palynomorphs and high proportions of amorphous organic matter in the lower parts of the siliciclastic intervals in the Hochalm Member (Holstein, 2004). Interestingly, the lower parts of the siliciclastic intervals correspond to the deepest habitats that were mainly occupied by epifaunal bivalves or brachiopods. In addition, barren beds in the siliciclastic intervals of the Eiberg Member were probably deposited under dysoxic or anoxic conditions, as indicated by very limited bioturbation, trace-element analyses and palynofacies

(Hüssner et al., 2000; Holstein, 2004). The decrease in oxygen concentrations can thus partly explain absence of infaunal suspension-feeding bivalves or of all shelly benthos in the siliciclastic intervals.

(5) Absence of infaunal bivalves due to low nutrient supply. Although the hypothesis about nutrient-supply control of brachiopod and bivalve communities due to their different metabolic demands is not new (Bambach, 1993), its application to soft-bottom habitats was not explicitly stated. The differential metabolic demands alone would not explain the abundance of epifaunal bivalves in soft-bottom habitats, as compared to the rarity of infaunal bivalves. However, the argument based on the actualistic evidence indicates that infaunal, mostly eulamellibranch, and epifaunal, mostly filibranch and pseudolamellibranch bivalves also differ in their feeding strategies with respect to low nutrient supply. During nutrient-poor carbonate regime, metabolic demands of infaunal suspension-feeding bivalves were probably not fulfilled and brachiopods and epifaunal bivalves thus dominated in soft-bottom habitats. This hypothesis is supported by low proportions of land-derived plant remains and microplankton in the carbonate intervals both in the Hochalm and Eiberg Member (Holstein, 2004). As land-derived nutrient supply decreases in offshore direction, this argument can be also used to explain the abundance of brachiopods and epifaunal bivalves and the concomitant scarcity of infaunal bivalves in deep soft-bottom habitats during nutrient-rich, siliciclastic regime (alternative hypothesis is that high input of siliciclastics and nutrients coupled with high plankton productivity caused hypoxia in the deepest habitats during siliciclastic regime).

The nutrient supply hypothesis is preferred here because variations in nutrient supply and turbidity can explain both the differential co-existence of guilds and their environmental distribution, although it can be supplemented by hypothesis with varying oxygen levels. For example, a combined effect of varying nutrient supply and oxygen concentrations was probably responsible for the scarcity of benthic fauna in the siliciclastic intervals of the Eiberg Member. Very high abundances of microplankton and land-derived plant remains (Holstein, 2004) indicate rather eutrophic conditions that would be favorable also for infaunal or semi-infaunal bivalves. However, restricted circulation coupled with high productivity in the Kössen Basin probably led to oxygen-deficient conditions, inhibiting both epifaunal and infaunal guilds.

The differential preferences of bivalves and brachiopods with respect to sediment and nutrient supply are supported by several studies. Miller (1988) found that the abundance and diversity of Paleozoic bivalves was substantially greater in siliciclastic than in carbonate habitats. Bambach (1993) thus suggested that the differential abundance of Paleozoic bivalves in carbonate and siliciclastic environments reflects a difference in quality and quantity of nutrient supply. Novack-Gottshall and Miller (2003a, b) found that bivalves were most diverse and numerically abundant in deep, siliciclastic-rich habitats during Ordovician. Patzkowsky (1995) observed that the Ordovician brachiopods were most abundant and diverse in carbonate rather than in siliciclastic habitats. Fürsich et al. (2001) and Gahr (2005) observed that brachiopods and epifaunal bivalves dominated and infaunal bivalves were relatively rare in habitats less affected by siliciclastic supply from land in the Lower Jurassic. In contrast, habitats affected by a higher siliciclastic supply were dominated by infaunal deposit-feeders and suspension-feeders.

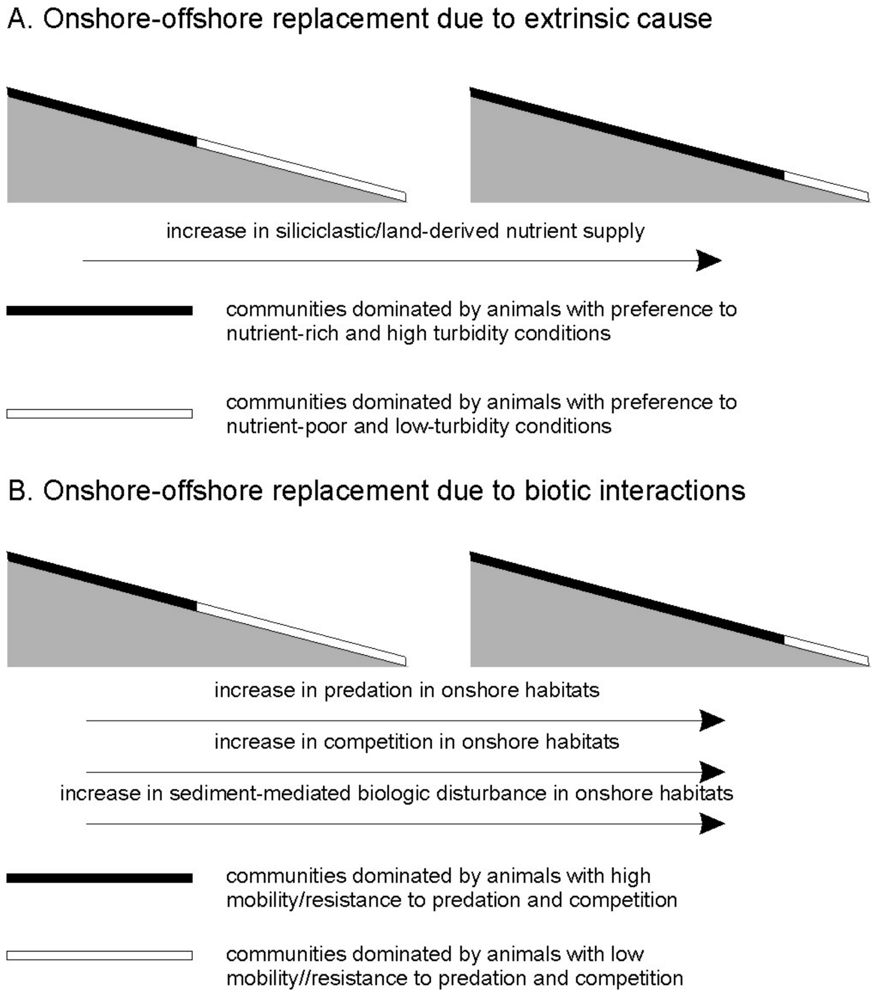


Figure 18 - Two scenarios for onshore-offshore replacements of benthic communities on short-time scale, without invoking evolutionary events (e.g., differential origination or extinction rates). In the first case, onshore communities expand because they track increased nutrient supply along an onshore-offshore gradient. In the second case, onshore communities expand into deeper habitats through increased competition ability, higher resistance to predation, or higher resistance to bioturbation.

Onshore-offshore expansions and retreats related to siliciclastic supply

Two end-member scenarios (Fig. 18) can be assumed for onshore-offshore replacements in marine habitats on short time-scale (i.e., about 10 to 100 ka) that do not need to invoke evolutionary events to explain them.

(1) Onshore-offshore replacement due to extrinsic causes: Animals with different environmental preferences change their position along an onshore-offshore gradient because they track extrinsically-induced variations in factors such as nutrient supply, turbidity or oxygen. Onshore-offshore replacements in the Kössen Formation are consistent with the differential response of bivalves and brachiopods to variations in nutrient supply and turbidity (Fig. 19). This scenario indicates that brachiopods in the Kössen Basin retreated offshore during siliciclastic-rich conditions because sedimentation rates and turbidity increased in onshore habitats. Infaunal and epifaunal bivalves seem to tolerate higher particle concentrations than brachiopods so they can occupy habitats with high siliciclastic supply. Infaunal eulamellibranch bivalves would retreat from offshore habitats during carbonate-rich conditions due to low nutrient supply. Very high nutrient input coupled with

water-column stratification could cause that low oxygen levels played also some role in restricting distribution of infaunal bivalves in offshore habitats, as is indicated by the siliciclastic intervals in the Eiberg Member.

(2) Onshore-offshore replacement due to biotic interactions: In this case, animals with different competitive ability or predation resistance are directly or indirectly restricted through biotic interactions. Therefore, this scenario infers that increased competition, increased predation pressure, and increased sediment-mediated biologic disturbance (Thayer, 1979, 1983; Vermeij, 1977, 1987, 1994) in onshore habitats lead to the exclusion of brachiopods and immobile epifaunal bivalves. Ideally, extrinsic environmental variations should be kept constant for testing the role of biotic interactions (Vermeij, 1987; Gotelli and Graves, 1996). It is possible that increased competition, predation or bioturbation correlated with increased nutrient supply because extrinsically-increased supply of energy and nutrients improves conditions for organisms with high metabolic demands on short time scales (Vermeij, 1995). For example, the increase in nutrient supply in onshore habitats would support abundant infaunal suspension-feeding bivalves and would thus indirectly lead to higher bioturbation, which can be deteriorating for poorly mobile epifaunal bivalves or brachiopods. The competitive ability of benthic animals with high metabolic demands would be also enhanced under increased nutrient-rich conditions. Although the presented results are inconclusive to evaluate the role of biotic interactions alone, the onshore-offshore replacements between bivalves and brachiopods in the Kössen Basin are also consistent with the scenario that brachiopod distribution is restricted via increased intensity of competition and bioturbation. However, the correlation of onshore-offshore replacements with changes in sediment and nutrient supply indicate that possible variations in competition, predation or bioturbation had to be coupled with variations in extrinsic factors.

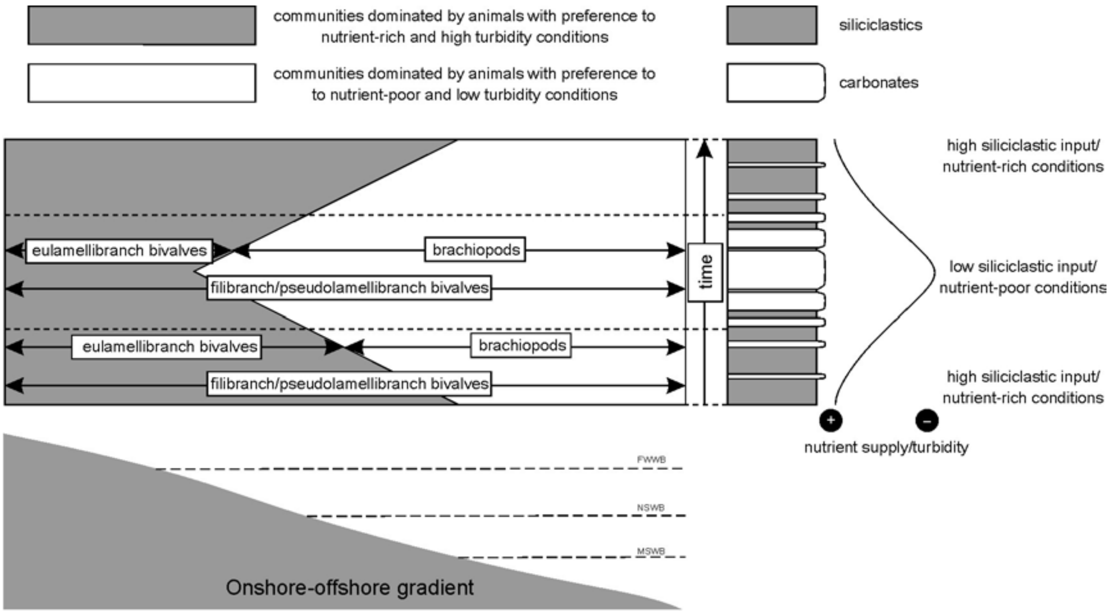


Figure 19 - The scenario for repeated onshore-offshore replacements caused primarily by variations in nutrient supply and turbidity, as applied to the Kössen Basin. The response of brachiopods and bivalves with different gill types is based on the interpreted replacements in the Kössen Basin and actualistic observations. Although variations in sedimentation rate can lead to relative sea level changes, bathymetric position of particular habitats is kept constant through time.

Onshore-offshore replacements on long time-scales

The Paleozoic and Modern faunas show an onshore-offshore replacement pattern through the Phanerozoic (Jablonski et al., 1983; Sepkoski and Miller, 1985; Bottjer and Jablonski, 1988; Sepkoski, 1991; Peters, 2004). Bottjer and Jablonski (1988) reviewed possible causes of onshore-offshore replacements. The two basic explanations involve either biotic or physical processes. Several studies demonstrated that varying predation, competition or bioturbation can influence the onshore-offshore replacements (e.g., Oji, 1996; Aronson et al., 1997; Dietl et al., 2000). Bottjer and Jablonski (1988) rejected the possibility that changes in physical processes can account for the onshore-offshore pattern, mainly because the timing of eustatic sea level changes and mass extinction events did not correlate with the timing of onshore-offshore replacements. Sepkoski and Miller (1985) also regarded changes in the physical environment as unlikely causes to account for onshore-offshore replacements of evolutionary faunas, mainly because it was not clear which environmental factor monotonically changed through the Phanerozoic.

Miller (1988) proposed that onshore-offshore expansion of Paleozoic bivalves might have been related to increased nutrient supply due to the rise of land plants (Calef and Bambach, 1973). The hypothesis of increased nutrient supply during the Devonian and Cretaceous, which enabled an increase in biomass, metabolic rates and productivity in marine habitats, was explored in detail by Bambach (1993, 1999). He also suggested that Phanerozoic offshore expansion of the modern evolutionary fauna, dominated by organisms with high metabolic demands, is related to this increase in nutrient supply. Although the onshore-offshore replacements in the Kössen Basin are on different time scale (Fig. 19), it is interesting to note that they are in accord with this hypothesis about variations in nutrient supply. However, in addition to different metabolic rates of brachiopods and bivalves, the difference in feeding strategies between epifaunal and infaunal suspension-feeding bivalves with roughly similar metabolic requirements was probably also important in governing their onshore-offshore distribution. Another explanation of onshore-offshore replacements on evolutionary time scale via extrinsic changes is related to varying degree of bottom oxygenation in offshore habitats through time (Jacobs and Lindberg, 1998). A net decrease in anoxic/dysoxic habitats since the Late Cretaceous can be complementary to Bambach`s scenario of offshore expansion of the modern evolutionary fauna. Although oxygen-deficient habitats are usually nutrient-rich, animals with high metabolic demands that lack adaptations to cope with low oxygen levels are inhibited in such conditions.

Conclusions

(1) This study shows that retreat of Late Triassic brachiopod communities from onshore habitats occurred repeatedly on short-time scale and was driven by variations in sediment and nutrient supply. In general, benthic communities dominated by brachiopods and bivalves show differential distribution patterns with respect to the proximity of siliciclastic and nutrient input. During regimes reflecting nutrient-poor, carbonate conditions, brachiopods co-occur with epifaunal bivalves above and below NSWB. Infaunal bivalves, if present, are restricted to shallowest depths above NSWB. In contrast, during nutrient-rich siliciclastic regimes, brachiopods and some epifaunal bivalves occur in the most distal habitats around MSWB, and infaunal and semi-infaunal bivalves are widespread above

and below NSWB. The offshore retreat of brachiopods and the offshore expansion of infaunal suspension-feeding bivalves thus coincide with the switch from a nutrient-poor, carbonate to a nutrient-rich, siliciclastic regime. Although the onshore to offshore expansion of infaunal bivalves at the expense of brachiopods during nutrient-rich conditions is also consistent with the hypothesis that brachiopods are restricted due to higher bioturbation and competition, any variations in intensity of biotic interactions were probably coupled with extrinsic variations in nutrient supply and turbidity.

(2) Although the replacements between infaunal and epifaunal communities may partly be due to variations in substrate quality, this cannot explain the whole pattern because brachiopods and epifaunal bivalves dominate also in micrite-rich bioturbated deposits. That brachiopods co-occur more commonly with epifaunal, mostly filibranch bivalves than with infaunal, mostly eulamellibranch bivalves is in accord with their more similar response to low nutrient supply in modern habitats. Abundance of poorly mobile epifaunal bivalves and brachiopods in soft-bottom, carbonate-rich habitats can be explained by nutrient-poor conditions which cannot support infaunal suspension-feeding bivalves with a high-energy metabolism and a less efficient feeding strategy. Abundance of poorly mobile epifaunal bivalves and brachiopods in deep, soft-bottom, siliciclastic-rich habitats can be explained either by decreased input of land-derived nutrients in offshore direction or by low oxygen levels in the deepest habitats due to restricted circulation.

Sample	GH1	TH2	TH3-1	TH3-2	GH3-3	TH4	TH5	TH6	TH7	GH8	GH9	GH10	TH11
Oxycolpella oxycolpos	0	0	0	0	0	0	0	0	0	0	0	0	0
Laballa suessi	0	0	0	0	0	0	0	0	0	0	0	0	0
Sinucosta emmrichi	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella uncinata	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella koessenensis	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhaetina gregaria	0	12	81	73	15	28	0	0	4	0	0	11	0
Rhaetina pyriformis	0	0	0	0	0	0	0	0	0	0	0	0	0
Triadithyris gregariaeformis	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Austrirhynchia cornigera	0	0	0	0	0	0	0	0	0	0	0	0	0
Fissirhynchia fissicostata	0	0	0	0	0	0	0	0	0	0	0	0	0
Calcirhynchia subrimosa	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhynchonellid sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculana claviformis	48	0	0	0	0	1	1	13	1	318	0	0	0
Parallelodon sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus minutus	0	0	1	0	0	0	0	0	0	0	0	0	2
Pteria sp. A	0	0	1	1	10	0	0	0	0	0	0	0	0
Rhaetavicula contorta	0	2	3	5	21	0	0	0	0	0	0	9	0
Gervillaria inflata	0	0	1	5	0	2	9	5	0	0	38	0	37
Bakevellia praecursor	21	0	7	0	0	0	26	5	29	62	0	0	0
Cassianella inaequiradiata	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma inequivalvis	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Propeamussium schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys coronata	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys sp.	0	1	0	0	0	0	0	0	0	0	0	8	0
Atreta intusstriata	0	5	3	0	163	0	0	0	0	0	0	57	1
Placunopsis alpina	8	0	4	4	0	0	0	0	2	10	9	0	0
Antiquilima alpis	0	0	0	0	0	0	0	0	0	0	0	0	0
Antiquilima sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma punctatum	0	0	0	0	0	0	0	0	0	0	0	2	0
Liostrea hinnities	0	1	0	0	12	0	0	0	1	0	0	3	0
Actinostreon haidingerianum	0	0	0	0	0	0	0	0	0	0	0	0	0
Gruenewaldia inflata	0	0	0	0	14	2	0	0	0	0	0	5	0
Myophoriopis isoceles	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudocorbula ewaldi	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita austriaca	0	0	0	0	36	0	0	0	0	0	21	19	3
Palaeocardita multiradiata	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia rhaetica	0	0	0	0	0	0	0	0	0	0	0	0	0
Homomya lagenalis	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Isocyprina alpina	238	0	0	0	0	0	34	44	29	1253	0	0	0
Mysidioptera waageni	0	0	0	0	0	0	0	0	0	0	0	0	0
Schafhaeutlia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalve indet A	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 - Absolute abundances of brachiopod and bivalve individuals in 74 samples from the Kössen Formation (MNI approach).

Sample	TH12	TH13-1	GH13-2	TH14	TH15	TH16	TH17	TH18	TH19	TH20	TH21	TH22	TH23
Oxycolpella oxycolpos	0	0	0	0	0	0	0	0	0	0	0	0	0
Laballa suessi	0	0	0	0	0	0	0	0	0	0	0	0	0
Sinucosta emmrichi	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella uncinata	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella koessenensis	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhaetina gregaria	0	22	56	0	0	0	0	0	0	0	0	0	0
Rhaetina pyriformis	0	0	0	0	0	0	0	0	0	0	10	0	2
Triadithyris gregariaeformis	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria sp.	0	0	0	0	0	0	0	0	0	0	0	1	7
Austrirhynchia cornigera	0	0	0	0	0	0	0	0	0	0	0	0	1
Fissirhynchia fissicostata	0	0	0	0	0	0	0	0	0	0	0	0	0
Calcirhynchia subrimosa	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhynchonellid sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculana claviformis	0	1	0	0	0	0	0	10	4	0	0	0	0
Parallelodon sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus minutus	0	0	0	0	0	8	0	0	0	0	0	0	0
Pteria sp. A	0	0	6	0	0	0	0	0	0	0	0	0	0
Rhaetavicula contorta	0	2	25	14	19	0	0	54	8	2	0	1	0
Gervillaria inflata	39	0	0	0	0	14	50	0	5	47	0	0	0
Bakevellia praecursor	0	0	0	35	2	0	0	15	0	0	0	0	0
Cassianella inaequiradiata	0	0	0	0	2	0	0	0	0	0	2	34	0
Pinna sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma inequivalvis	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Propeamussium schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys coronata	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys sp.	1	2	0	0	0	0	0	0	0	0	2	0	8
Atreta intusstriata	0	18	90	0	0	0	0	0	0	0	1	0	4
Placunopsis alpina	1	0	0	0	0	0	0	10	1	0	0	1	0
Antiquilima alpis	0	0	0	0	0	0	0	0	0	0	0	0	0
Antiquilima sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma punctatum	0	0	8	0	0	0	0	0	0	0	3	0	1
Liostrea hinnities	0	1	32	0	0	7	0	0	0	0	0	0	0
Actinostreon haidingerianum	0	0	0	0	0	0	0	0	0	0	0	0	0
Gruenewaldia inflata	0	0	2	0	0	0	0	0	0	0	0	0	0
Myophoriopis isoceles	0	0	0	0	18	0	3	4	16	0	0	0	0
Pseudocorbula ewaldi	0	0	0	4	0	0	0	3	0	0	0	0	0
Palaeocardita austriaca	5	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita multiradiata	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita sp. A	0	0	0	0	0	0	0	1	0	0	0	0	0
Protocardia rhaetica	0	1	0	0	1	0	0	5	5	0	0	0	0
Homomya lagenalis	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Isocyprina alpina	0	0	0	0	0	0	8	0	2	0	0	0	0
Mysidioptera waageni	0	0	0	0	0	0	0	0	0	0	0	0	0
Schafhaeutlia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalve indet A	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 (cont.)

Sample	TE1	TE2	TE3	TE4	TE5	TE6	TE7	TE8	TE9	TE10	TE11	TE12	TE13
Oxycolpella oxycolpos	0	0	0	0	0	0	0	0	0	0	0	0	0
Laballa suessi	0	0	0	0	0	0	0	0	0	0	0	0	0
Sinucosta emmrichi	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella uncinata	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella koessenensis	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhaetina gregaria	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhaetina pyriformis	0	0	0	0	0	0	0	0	0	0	0	0	38
Triadithyris gregariaeformis	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria sp.	0	0	0	0	0	0	0	0	0	0	0	0	9
Austrirhynchia cornigera	0	0	0	0	0	0	0	0	0	0	0	0	0
Fissirhynchia fissicostata	0	0	0	0	0	0	0	0	0	0	0	0	0
Calcirhynchia subrimosa	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhynchonellid sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculana claviformis	0	0	0	0	0	0	0	0	0	0	0	0	0
Parallelodon sp. A	0	1	0	0	0	0	0	1	0	2	0	5	0
Grammatodon sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	2
Modiolus minutus	0	0	0	0	0	0	1	0	0	1	1	0	1
Pteria sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhaetavicula contorta	0	17	0	3	0	0	0	18	14	58	5	2	0
Gervillaria inflata	0	21	3	3	21	57	64	4	9	0	2	0	0
Bakevellia praecursor	0	0	0	0	0	0	0	0	0	0	0	0	0
Cassianella inaequiradiata	51	0	0	0	0	0	0	0	1	3	2	1	0
Pinna sp. A	0	0	0	0	0	0	0	0	0	0	0	0	1
Oxytoma inequivalvis	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Propeamussium schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys coronata	0	0	0	0	0	0	0	0	0	9	3	0	0
Chlamys sp.	0	0	0	0	0	0	0	0	0	0	0	2	6
Atreta intusstriata	0	0	6	0	0	0	0	3	0	1	0	0	0
Placunopsis alpina	0	33	2	0	3	1	10	4	0	0	0	3	0
Antiquilima alpis	0	0	0	0	0	0	0	0	0	0	0	0	0
Antiquilima sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma punctatum	0	1	0	0	0	0	0	0	0	0	0	0	1
Liostrea hinnities	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon haidingerianum	0	0	0	0	0	0	0	0	0	0	0	0	2
Gruenewaldia inflata	0	1	0	0	0	0	0	0	0	0	0	0	0
Myophoriopis isoceles	19	0	4	28	0	0	0	17	21	64	40	5	0
Pseudocorbula ewaldi	2	18	1	10	0	0	3	0	1	10	13	0	0
Palaeocardita austriaca	0	0	0	0	0	0	0	0	0	0	0	1	0
Palaeocardita multiradiata	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita sp. A	1	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia rhaetica	15	1	2	0	0	0	0	11	7	23	5	9	0
Homomya lagenalis	0	0	0	0	0	0	0	0	1	0	0	0	0
Pleuromya sp. A	0	0	0	0	0	0	0	0	0	0	0	2	0
Isocyprina alpina	0	3	0	0	0	1	0	7	0	0	0	0	0
Mysidioptera waageni	0	0	0	0	0	0	0	0	0	0	0	0	3
Schafhaeutlia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalve indet A	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 (cont.)

Sample	TE14	TE15	TE16	TE17	TE18	TE19	TK1	TK2	GK3	TK4	TK5	TK6	TK7
Oxycolpella oxycolpos	2	0	0	2	15	35	0	0	0	0	0	0	0
Laballa suessi	0	0	0	0	1	0	0	0	0	0	0	0	0
Sinucosta emmrichi	0	3	0	0	11	0	0	0	0	0	0	0	0
Zugmayerella uncinata	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella koessenensis	0	4	1	0	0	3	0	0	0	0	0	0	0
Rhaetina gregaria	0	0	0	0	0	0	17	1	0	0	0	0	0
Rhaetina pyriformis	0	0	0	0	0	0	0	0	0	0	0	0	0
Triadithyris gregariaeformis	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria sp.	5	0	0	0	0	0	0	0	0	0	0	0	0
Austrirhynchia cornigera	0	0	0	1	0	0	0	0	0	0	0	0	0
Fissirhynchia fissicostata	0	25	0	6	1	3	0	0	0	0	0	0	0
Calcirhynchia subrimosa	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhynchonellid sp. A	3	0	77	0	0	0	0	0	0	0	0	0	0
Nuculana claviformis	0	0	0	0	0	0	0	8	132	0	0	0	0
Parallelodon sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	3	0
Modiolus minutus	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria sp. A	0	0	0	0	0	0	0	0	0	1	0	0	0
Rhaetavicula contorta	0	0	0	0	0	0	0	0	0	8	3	9	7
Gervillaria inflata	0	0	0	0	0	0	15	5	0	0	11	0	0
Bakevellia praecursor	0	0	0	0	0	0	0	43	279	56	0	0	0
Cassianella inaequiradiata	0	0	0	0	1	0	0	0	0	0	0	0	0
Pinna sp. A	0	1	0	0	0	0	0	0	0	0	0	0	2
Oxytoma inequivalvis	0	9	1	0	1	0	0	0	0	0	0	0	0
Entolium sp. A	0	0	0	1	0	0	0	0	0	0	0	2	0
Propeamussium schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys coronata	0	0	0	0	0	0	0	0	0	0	0	23	4
Chlamys sp.	1	1	1	1	0	0	0	0	0	1	1	1	0
Atreta intusstriata	0	3	0	0	0	1	0	0	0	1	0	1	1
Placunopsis alpina	0	0	0	0	0	0	0	3	23	0	10	3	0
Antiquilima alpis	0	0	0	0	0	0	0	0	0	3	0	0	0
Antiquilima sp. A	0	0	0	0	0	0	0	0	0	1	0	0	0
Plagiostoma punctatum	0	0	0	0	0	0	0	0	0	0	0	0	1
Liostrea hinnities	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon haidingerianum	0	0	0	0	0	0	0	0	0	0	0	0	0
Gruenewaldia inflata	0	0	0	0	0	0	0	0	0	0	0	0	0
Myophoriopis isoceles	0	0	0	0	0	0	2	0	0	3	12	0	0
Pseudocorbula ewaldi	0	0	0	0	0	0	0	0	0	0	4	0	0
Palaeocardita austriaca	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita multiradiata	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia rhaetica	0	0	0	0	0	0	0	0	0	0	4	0	8
Homomya lagenalis	0	0	0	0	0	0	0	0	0	0	0	0	6
Pleuromya sp. A	0	0	0	0	0	0	0	0	0	0	1	0	0
Isocyprina alpina	0	0	0	0	0	0	0	42	343	0	3	0	0
Mysidioptera waageni	0	0	0	0	0	0	0	0	0	0	0	0	0
Schafhaeutlia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalve indet A	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 (cont.)

Sample	TK8	TK9	TK10	TK11	TK12	TG1	TG2	TG3	TG4	TG5	TG6	TG7	TG8
Oxycolpella oxycolpos	0	1	27	0	0	0	0	0	0	0	0	0	0
Laballa suessi	0	0	1	0	0	0	0	0	0	0	0	0	0
Sinucosta emmrichi	0	1	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella uncinata	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella koessenensis	0	2	2	0	0	0	0	0	0	0	0	3	3
Rhaetina gregaria	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhaetina pyriformis	25	0	0	0	0	0	0	0	0	0	0	0	0
Triadithyris gregariaeformis	3	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria sp.	12	11	3	0	2	0	0	0	0	0	0	4	2
Austrirhynchia cornigera	1	5	0	0	0	0	0	0	0	0	0	0	0
Fissirhynchia fissicostata	0	0	6	0	0	0	0	0	0	0	0	5	7
Calcirhynchia subrimosa	0	15		60	37	0	0	0	0	0	0	0	0
Rhynchonellid sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculana claviformis	0	0	0	0	0	0	0	0	3	0	0	0	0
Parallelodon sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon sp. A	3	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus minutus	7	0	0	0	0	0	0	0	0	0	0	0	0
Pteria sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhaetavicula contorta	0	0	0	0	0	0	6	174	23	15	0	0	0
Gervillaria inflata	0	0	0	0	0	57	0	2	2	1	17	0	0
Bakevellia praecursor	0	0	0	0	0	0	0	0	0	0	0	0	0
Cassianella inaequiradiata	0	1	0	0	0	0	0	0	0	0	0	0	1
Pinna sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma inequivalvis	0	2	0	13	8	0	0	0	0	0	0	0	0
Entolium sp. A	0	0	0	1	1	0	0	0	0	0	0	0	0
Propeamussium schafhaeutli	1	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys coronata	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys sp.	4	0	1	3	1	0	2	3	0	1	0	0	0
Atreta intusstriata	5	0	0	0	0	0	37	6	0	0	0	1	2
Placunopsis alpina	1	0	0	0	0	0	0	7	2	1	0	0	0
Antiquilima alpis	0	0	0	0	0	0	0	1	0	0	0	0	0
Antiquilima sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma punctatum	5	0	0	0	0	0	0	0	0	0	0	1	2
Liostrea hinnities	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon haidingerianum	4	0	0	0	0	0	0	0	0	0	0	0	0
Gruenewaldia inflata	0	0	0	0	0	0	0	0	0	0	0	0	0
Myophoriopis isoceles	0	0	0	0	0	0	4	16	13	17	0	0	0
Pseudocorbula ewaldi	0	0	0	0	0	0	0	0	0	6	0	0	0
Palaeocardita austriaca	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita multiradiata	1	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia rhaetica	0	0	0	0	0	0	2	0	5	16	0	0	0
Homomya lagenalis	1	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Isocyprina alpina	0	0	0	0	0	0	0	0	0	0	0	0	0
Mysidioptera waageni	0	0	0	0	0	0	0	0	0	0	0	0	0
Schafhaeutlia sp.	0	0	0	0	0	0	0	0	0	0	0	0	1
Bivalve indet A	0	0	0	0	0	0	0	0	0	0	0	0	1

Appendix 1 (cont.)

Sample	TG9	TSA1	TSA2	TSC2	TSC1	TSC4	TSC5	GN24	GHS5
Oxycolpella oxycolpos	0	0	0	0	0	0	0	0	0
Laballa suessi	0	0	0	0	0	0	0	0	0
Sinucosta emmrichi	0	0	0	0	0	1	0	0	0
Zugmayerella uncinata	0	0	0	5	11	0	0	0	0
Zugmayerella koessenensis	0	0	6	0	0	0	7	0	0
Rhaetina gregaria	0	5	0	15	0	2	0	0	0
Rhaetina pyriformis	0	7	15	13	0	6	0	0	0
Triadithyris gregariaeformis	0	0	1	0	0	0	0	0	0
Zeilleria sp.	5	10	11	14	8	3	3	0	0
Austrirhynchia cornigera	0	1	7	0	1	1	1	0	0
Fissirhynchia fissicostata	79	0	7	9	0	0	0	0	0
Calcirhynchia subrimosa	0	0	0	0	0	0	0	0	0
Rhynchonellid sp. A	5	0	0	0	0	0	0	0	0
Nuculana claviformis	0	0	0	0	0	0	0	0	17
Parallelodon sp. A	0	0	0	0	0	0	0	0	0
Grammatodon sp. A	0	0	0	0	0	0	0	0	0
Inoperna schafhaeutli	0	0	0	0	0	0	0	0	0
Modiolus minutus	0	0	0	2	0	0	0	0	0
Pteria sp. A	0	0	0	0	0	0	0	0	0
Rhaetavicula contorta	0	0	0	0	0	0	0	0	0
Gervillaria inflata	0	1	13	0	0	3	0	82	0
Bakevellia praecursor	0	0	0	0	0	0	0	0	11
Cassianella inaequiradiata	0	0	0	0	1	1	0	0	0
Pinna sp. A	0	0	1	0	0	1	1	0	0
Oxytoma inequivalvis	10	0	0	0	0	0	1	0	0
Entolium sp. A	1	0	0	0	0	0	0	0	0
Propeamussium schafhaeutli	0	0	0	0	0	0	0	0	0
Chlamys coronata	0	0	0	0	0	0	0	0	0
Chlamys sp.	7	4	2	1	22	2	0	0	0
Atreta intusstriata	0	0	1	0	0	0	1	0	0
Placunopsis alpina	0	0	1	1	0	0	0	0	5
Antiquilima alpis	0	0	0	0	0	0	0	0	0
Antiquilima sp. A	0	0	0	0	0	0	0	0	0
Plagiostoma punctatum	0	1	2	1	18	0	0	0	0
Liostrea hinnities	0	0	0	1	2	0	0	8	0
Actinostreon haidingerianum	0	3	1	4	0	1	0	0	0
Gruenewaldia inflata	0	0	0	0	0	0	0	0	0
Myophoriopis isoceles	0	0	1	0	0	0	0	0	0
Pseudocorbula ewaldi	0	0	0	0	0	0	0	0	0
Palaeocardita austriaca	0	0	0	0	0	0	0	21	0
Palaeocardita multiradiata	0	0	0	0	0	0	0	0	0
Palaeocardita sp. A	0	0	0	0	1	0	0	0	0
Protocardia rhaetica	0	0	0	1	0	0	0	0	0
Homomya lagenalis	0	0	0	0	0	0	0	0	0
Pleuromya sp. A	0	0	1	0	0	1	0	0	0
Isocyprina alpina	0	0	0	0	0	0	0	0	137
Mysidioptera waageni	0	1	1	0	0	0	0	0	0
Schafhaeutlia sp.	0	0	0	0	0	0	0	0	0
Bivalve indet A	0	2	0	0	0	0	0	0	0

Appendix 1 (cont.)

Sample	Sample group	Member	Interval	Depth
GH1	*Isocyprina*	2	siliciclastic	below NSWB
TH2	*R. gregaria*	2	carbonate	above NSWB
TH3-1	*R. gregaria*	2	carbonate	above NSWB
TH3-2	*R. gregaria*	2	carbonate	above NSWB
GH3-3	*R. gregaria*	2	carbonate	above NSWB
TH4	*R. gregaria*	2	claystone	below NSWB
TH5	*Isocyprina*	2	siliciclastic	below NSWB
TH6	*Isocyprina*	2	siliciclastic	below NSWB
TH7	*Isocyprina*	2	siliciclastic	below NSWB
TH8	*Isocyprina*	2	siliciclastic	below NSWB
TH9	*Gervillaria*	2	siliciclastic	above NSWB
GH10	*R. gregaria*	2	limestone	above NSWB
TH11	*Gervillaria*	2	siliciclastic	below NSWB
TH12	*Gervillaria*	2	siliciclastic	below NSWB
TH13-1	*R. gregaria*	2	limestone	below NSWB
GH13-2	*R. gregaria*	2	limestone	below NSWB
TK1	*R. gregaria*	2	siliciclastic	below NSWB
TK2	*Isocyprina*	2	siliciclastic	below NSWB
TK3	*Isocyprina*	2	siliciclastic	below NSWB
GN24	*Gervillaria*	2	siliciclastic	no data
GHS5	*Isocyprina*	2	siliciclastic	no data
TH16	*Gervillaria*	3	siliciclastic	above NSWB
TH14	*Bakevellia*	3	carbonate	above NSWB
TH15	*Myophoriopis*	3	siliciclastic	below NSWB
TH17	*Gervillaria*	3	siliciclastic	above NSWB
TH18	*Myophoriopis*	3	carbonate	above NSWB
TH19	*Myophoriopis*	3	carbonate	above NSWB
TH20	*Gervillaria*	3	siliciclastic	below NSWB
TH21	*R. pyriformis*	3	carbonate	below NSWB
TH22	*Cassianella*	3	siliciclastic	below MSWB
TE1	*Cassianella*	3	siliciclastic	below MSWB
TE2	*Myophoriopis*	3	carbonate	above NSWB
TE3	*Myophoriopis*	3	carbonate	above NSWB
TE4	*Myophoriopis*	3	siliciclastic	below NSWB
TE5	*Gervillaria*	3	siliciclastic	above NSWB
TE6	*Gervillaria*	3	siliciclastic	above NSWB
TE7	*Gervillaria*	3	siliciclastic	above NSWB
TE8	*Myophoriopis*	3	carbonate	above NSWB
TE9	*Myophoriopis*	3	carbonate	above NSWB
TE10	*Myophoriopis*	3	siliciclastic	below NSWB
TE11	*Myophoriopis*	3	siliciclastic	below NSWB
TE12	*Myophoriopis*	3	carbonate	below NSWB
TK4	*Bakevellia*	3	siliciclastic	below NSWB
TK5	*Myophoriopis*	3	carbonate	below NSWB
TK6	*Chlamys*	3	siliciclastic	below MSWB
TK7	*Chlamys*	3	siliciclastic	below MSWB
TK8	*R. pyriformis*	3	carbonate	below NSWB
TG1	*Gervillaria*	3	siliciclastic	above NSWB
TG2	*R. gregaria*	3	siliciclastic	below MSWB
TG3	*Myophoriopis*	3	siliciclastic	below NSWB
TG4	*Myophoriopis*	3	siliciclastic	below NSWB
TG5	*Myophoriopis*	3	siliciclastic	below NSWB
TG6	*Gervillaria*	3	siliciclastic	above NSWB
TH23	*R. pyriformis*	4	carbonate	below NSWB
TE13	*R. pyriformis*	4	carbonate	below NSWB
TE14	Rhynchonellid A	6-7	carbonate	below MSWB
TE15	*Fissirhynchia*	6-7	carbonate	below MSWB
TE16	Rhynchonellid A	6-7	carbonate	below MSWB
TE17	*Fissirhynchia*	6-7	carbonate	below MSWB
TE18	*Oxycolpella*	6-7	carbonate	below MSWB
TE19	*Oxycolpella*	6-7	carbonate	below MSWB
TK9	*Zugmayerella*	6-7	carbonate	below MSWB
TK10	*Oxycolpella*	6-7	carbonate	below MSWB
TK11	*Calcirhynchia*	6-7	carbonate	below MSWB
TK12	*Calcirhynchia*	6-7	carbonate	below MSWB
TG7	*Zugmayerella*	4	carbonate	above NSWB
TG8	*Zugmayerella*	4	carbonate	above NSWB
TG9	*Fissirhynchia*	5	carbonate	below MSWB
TSA1	*R. pyriformis*	4	carbonate	above NSWB
TSA2	*R. pyriformis*	4	carbonate	above NSWB
TSC2	*R. pyriformis*	4	carbonate	above NSWB
TSC1	*R. pyriformis*	4	carbonate	below NSWB
TSC4	*R. pyriformis*	4	carbonate	above NSWB
TSC5	*Zugmayerella*	4	carbonate	above NSWB

Appendix 2 - Assignments of samples to stratigraphic units, intervals and habitats.

Taxon	Guild
Oxycolpella oxycolpos	free-lying brachiopod
Laballa suessi	pedunculate brachiopod
Sinucosta emmrichi	pedunculate brachiopod
Zugmayerella uncinata	pedunculate brachiopod
Zugmayerella koessenensis	pedunculate brachiopod
Rhaetina gregaria	pedunculate brachiopod
Rhaetina pyriformis	pedunculate brachiopod
Triadithyris gregariaeformis	pedunculate brachiopod
Zeilleria sp.	pedunculate brachiopod
Austrirhynchia cornigera	pedunculate brachiopod
Fissirhynchia fissicostata	pedunculate brachiopod
Calcirhynchia subrimosa	free-lying brachiopod
Rhynchonellid sp. A	free-lying brachiopod
Nuculana claviformis	shallow burrowing deposit-feeder
Parallelodon sp. A	epibyssate filibranch
Grammatodon sp. A	epibyssate filibranch
Inoperna schafhaeutli	endobyssate filibranch
Modiolus minutus	endobyssate filibranch
Pteria sp. A	epibyssate filibranch
Rhaetavicula contorta	epibyssate filibranch
Gervillaria inflata	endobyssate filibranch
Bakevellia praecursor	endobyssate filibranch
Cassianella inaequiradiata	free-lying filibranch
Pinna sp. A	endobyssate filibranch
Oxytoma inequivalvis	epibyssate filibranch
Entolium sp. A	free-lying filibranch
Propeamussium schafhaeutli	free-lying filibranch
Chlamys coronata	epibyssate filibranch
Chlamys sp. A	epibyssate filibranch
Atreta intusstriata	cementing filibranch
Placunopsis alpina	cementing filibranch
Antiquilima alpis	epibyssate filibranch
Antiquilima sp. A	epibyssate filibranch
Plagiostoma punctatum	epibyssate filibranch
Liostrea hinnities	cementing filibranch
Actinostreon haidingerianum	free-lying pseudolamellibranch
Gruenewaldia inflata	shallow burrowing filibranch
Myophoriopis isoceles	shallow burrowing eulamellibranch
Pseudocorbula ewaldi	shallow burrowing eulamellibranch
Palaeocardita austriaca	shallow burrowing eulamellibranch
Palaeocardita multiradiata	shallow burrowing eulamellibranch
Palaeocardita sp. A	shallow burrowing eulamellibranch
Protocardia rhaetica	shallow burrowing eulamellibranch
Homomya lagenalis	deep burrowing eulamellibranch
Pleuromya sp. A	deep burrowing eulamellibranch
Isocyprina alpina	shallow burrowing eulamellibranch
Mysidioptera waageni	epibyssate filibranch
Schafhaeutlia sp.	shallow burrowing eulamellibranch
Large bivalve A	deep burrowing eulamellibranch

Appendix 3 - Assignments of brachiopods and bivalves to guilds.

4. Ecology of brachiopods and bivalves in the Upper Triassic of the Fatric Unit (West Carpathians)

Abstract. Benthic communities dominated by brachiopods and bivalves inhabited a relatively shallow, mixed, carbonate-siliciclastic intra-shelf Fatric Basin, which was situated within an extensive carbonate platform on the northwestern margin of the Tethys Ocean. In term of Bray-Curtis similarities, pedunculate brachiopods co-occurred more commonly with epifaunal, filibranch and pseudolamellibranch bivalves than with infaunal eulamellibranch bivalves. Abundance patterns of pedunculate brachiopods differ significantly from abundance patterns of eulamellibranch and filibranch bivalves. Environmental analyses imply that distribution of brachiopods and bivalves was governed by variations in siliciclastic supply, wave-base level and substrate consistency. Brachiopods increased in abundance towards deeper habitats and were mainly abundant in mixed-bottom habitats with marly sediments. Epifaunal bivalves increased in abundance towards shallower, carbonate-rich and hard-bottom habitats. Infaunal bivalves increased in abundance with increasing siliciclastic supply, and were mainly common at intermediate depths in mixed- and soft-bottom habitats. Onshore-offshore distribution patterns of brachiopods and bivalves substantially changed within depositional sequences between intervals characterized by shoreline retrogradation and progradation. Brachiopods dominated both in shallow and deep habitats during shoreline retrogradation owing to relatively rapid sea level rise. This phase was also characterized by onset of coral communities. In contrast, bivalves dominated in shallow and deep habitats mainly during shoreline progradation. Within-sequence replacement thus implies that varying nutrient and siliciclastic supply might govern environmental segregation of brachiopods and bivalves. Differences in distribution patterns between brachiopods and bivalves are comparable to those observed in the Kössen Basin and can be explained by actualistic hypotheses that are based on differences in their physiology and feeding strategies. Dominance of brachiopods in soft-bottom habitats can be explained by varying levels of turbidity and land-derived nutrient supply that were reduced during rapid shoreline retrogradation. Reduced food supply might account for low abundance of infaunal bivalves and thus reduced sediment disturbance in soft-bottom habitats under transgressive conditions.

Introduction

During the Late Triassic, the northwestern shelf of the Tethys Ocean was inhabited by communities rich in brachiopods and bivalves. Stratigraphic successions in the Southern Alps, Eastern Alps and Western Carpathians record various depositional environments differing in the composition of benthic communities. This enables to track relationships between environmental variables and abundances of benthic fauna, and to evaluate whether and what environmental factors correlate with brachiopod and bivalve distribution patterns. One of the qualitative impressions that stems from distribution patterns of brachiopods and bivalves in the Late Triassic environments is that they dominated in different environments (Michalík and Jendrejáková, 1978; Golebiowski, 1991). To address whether environmental factors controlled abundances of brachiopods and bivalves in distinct basins in similar ways, their ecology was evaluated in the Kössen Basin (Chapter 3), in the Fatric Basin (this chapter) and in the Hronic Basin (Chapter 5). The purpose of this chapter is to describe benthic communities of the Fatric Basin, to evaluate whether brachiopod and bivalve communities differ in the alpha diversity, to test whether brachiopod and bivalve guilds differ in abundance patterns, and to assess whether and to what degree environmental factors governed their distribution patterns. The emphasis is on factors that may explain with environmental separation between communities dominated by brachiopods and bivalves, and on the conditions that enabled dominance of brachiopods in soft-bottom habitats (i.e., what factors caused sediment stability or low levels of bioturbation in such habitats).

Figure 1 - Geographic maps of the study area. A. Regional map with location of ten stratigraphic sections. B. Geographic location of six sections in the Veľká Fatra Mountains.

Setting and sections

Setting. Depositional environments of the Western Carpathians belonged to the carbonate platform on the northwestern margin of the Tethys Ocean in the Late Triassic (Michalík 1994; Gawlick 2000). This carbonate platform was subdivided into several shore-parallel environments. The most proximal nearshore zone was formed by continental deposits (Tatric Unit). To the south, this zone was followed by the intra-platform, carbonate-dominated Fatric Basin (Fatric Unit), by a carbonate platform with restricted peritidal and lagoonal environments and deeper embayments (Veporic, Hronic and Silicic units), and finally by rimming Dachstein-reefs (Silicic Unit). During the Rhaetian, the Fatric Basin was characterized by deposition of the Fatra Formation (Michalík 1973b, 1977a, 1982, Tomašových, 2004a, b). The Fatric Basin was connected with the Tethys Ocean either via the shallow carbonate platform top, or through a system of deeper intra-shelf basins formed by the depositional environments of the Hronic Basin (Hronic Unit) and Kössen Basin (Tirolic Unit of the Eastern Alps).

Sections. Ten stratigraphic sections of the Fatra Formation (Rhaetian) that belong to the Fatric Unit (Krížna Nappe, West Carpathians) were analyzed. Seven carbonate-rich sections with the completely or partly exposed Fatra Formation are situated in the Veľká Fatra and Malá Fatra mountains (central Slovakia, Fig. 1). They are about 40 meters thick and represent an approximately 50-km long, N-S oriented transect through the intra-shelf basin of the Fatric Unit. The Veľká Furkaška section is situated in the West Tatra Mountains (northern Slovakia) and is characterized by comparable thickness and stratigraphic features. All these sections are characterized by dominance of limestone beds, very low proportions of terrigenous admixture and low thickness of marlstones. Two sections with higher proportions of terrigenous admixture and different stratigraphic features are situated in the Belianske Tatry Mountains (northern Slovakia). They were probably situated closely to a continental source of siliciclastic supply, in contrast to carbonate-rich sections that represent a typical facies succession of the Fatra Formation in the Fatric Basin.

Eight sections in the Veľká Fatra, Malá Fatra and West Tatra Mountains were subdivided into four stratigraphic sequences (sequences 1-4) that are separated by unconformities (Tomašových 2004a). These sequences and unconformities can be correlated across most of the sections (Fig. 2). The stratigraphic sequences consist of small-scale, lagoonal-peritidal or lagoonal-skelektal bank shallowing-upward parasequences. The unconformities cap the shallowest deposits, which are represented by mudstones, bindstones and well sorted ooidal, intraclastic and bioclastic grainstones. The middle parts of sequences 1 and 3 are characterized relatively abrupt retrogradation of skeletal banks, implying intervals of maximum deepening. About 4-5 m above the base of Sequence 1, an abrupt replacement of bioclastic, ooidal and intraclastic grainstones and rudstones with mollusks by wackestones and floatstones with brachiopods, corals and sponges marks this interval (Fig. 2). The upper part of Sequence 1 is characterized by high abundance of dm-scale thickets and meter-scale patch-reefs with branching corals (*Retiophyllia*). The coral beds are laterally replaced by well sorted bioclastic, ooidal and intraclastic packstones and grainstones (Fig. 2). The uppermost parts of Sequence 1 are formed by peritidal mudstones, bindstone or skeletal banks that are capped by the unconformity. The base of Sequence 2 is characterized by 2-3-m thick, bimodally-sorted packstones with dispersed, commonly overturned coral colonies and megalodonts. The boundary interval between sequences 2 and 3 is formed by a group of laminated, locally dolomitic mudstones or dolomites that are capped by the unconformity and overlain by well sorted packstones/grainstones. Sequence 3 is characterized by variable facies associations. In the middle parts, low-energy brachiopod floatstones and packstones replace peritidal mudstones or high-energy skeletal banks. In the upper parts, Sequence 3 is capped by an about 1-m thick interval of dolomites. About 3-4-m thick Sequence 4 consists of small-scale shallowing upward parasequences and is sharply replaced by siltstones of the Kopienec Formation (Hettangian). In sequence stratigraphic terms, the sequence boundaries are assumed to represent the shallowest conditions that reflect maximum rate of sediment progradation. The rapid retrogradation of shallow-water sediments marked in the middle parts of sequences 1 and 3 is supposed to reflect maximum flooding intervals with reduced rate of siliciclastic sedimentation and reduced input of carbonate sediment from shallow areas.

The Žďiarska Vidla section represents one of the most landward-situated sections of the Fatric Unit and its thickness is reduced to 15 m. The lower part reflects the replacement of bivalve by brachiopod- and coral-dominated communities and is thus comparable to other carbonate-rich sections of the Fatra Formation. The upper part of the section is distinctive because it contains a high amount of siliciclastic, mainly sandy admixture (Fig. 2). The Kardolína section is more than 80-m thick and is characterized by high proportions of thick marlstones in its lower, 25-m thick part (Fig. 3). In this part, marlstones alternate with storm-reworked floatstones and packstones with complex internal stratifications, and with grainstones/rudstones that form small-scale skeletal banks. Several meters thick crinoidal and ooidal packstones/grainstones representing bioclastic or oolite bars dominate in the middle, about 45-m thick carbonate-rich part of the section. These bars are separated by four intervals of coral framestones, coral debris floatstones with red algae, and brachiopod floatstones (Fig. 3). The upper part of the section is formed by alternation of bioclastic floatstones with marlstones with abundant bivalves.

Stratigraphy. The first occurrence datum of brachiopod *Austrirhynchia cornigera* is present about 4-5 meters above the lower boundary of the Fatra Formation. The first occurrence of *Austrirhynchia cornigera* in the Kössen Basin correlates with an onset of the *Vandaites sturzenbaumi* Zone (Golebiowski 1990). It is thus probable that the Fatra Formation corresponds to the *Vandaites sturzenbaumi* and *Choristoceras marshi* zones.

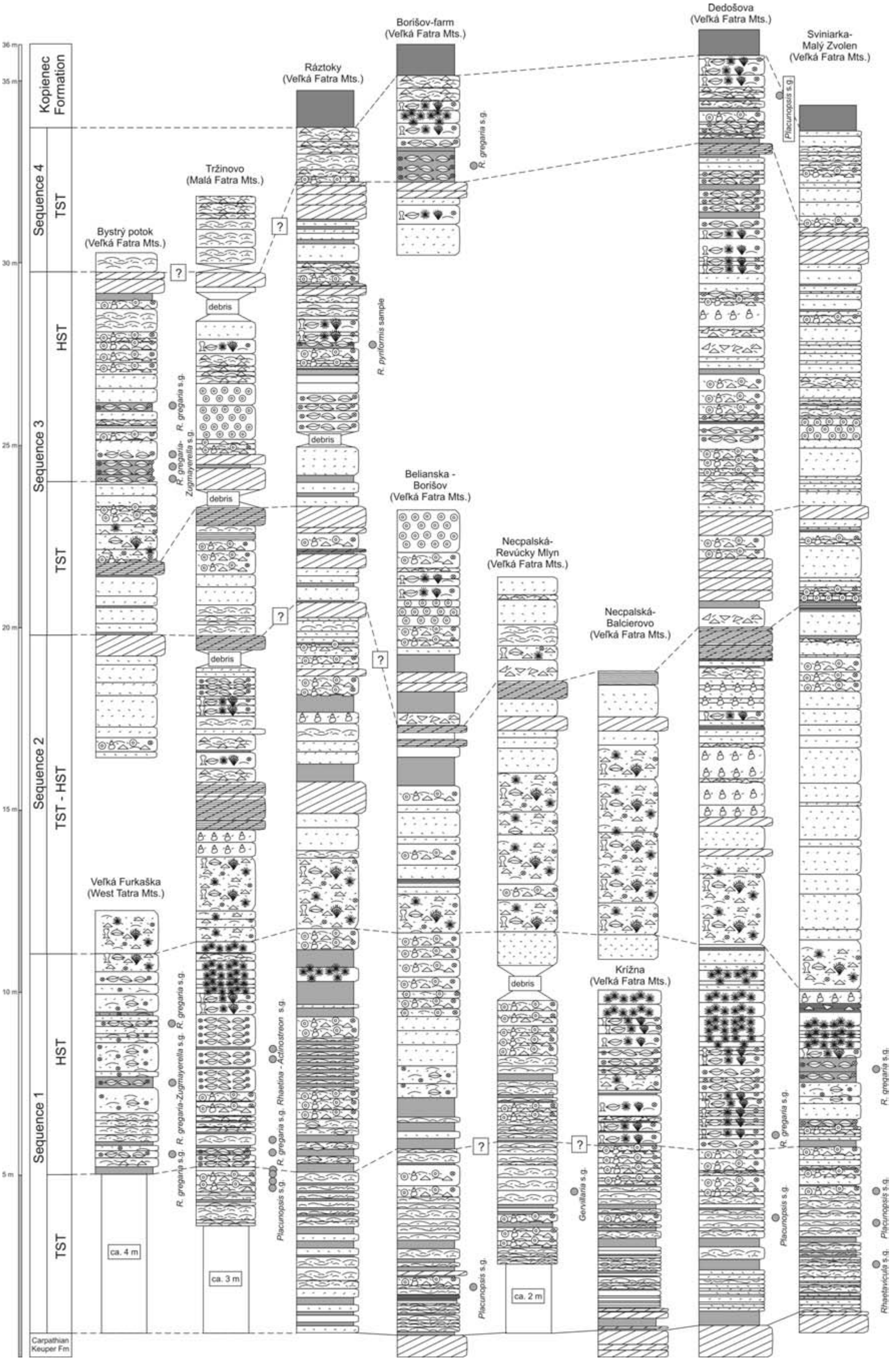


Figure 2 - Stratigraphic sequences and distribution of sample groups of the Fatra Formation in the Veľká Fatra, Malá Fatra and West Tatra mountains. Explanations: see Figure 3.

Methods

Bivalves were classified into ten guilds according to their substrate relationship (Aberhan 1994) and gill type (Stanley 1968; Waller, 1998), and brachiopods into a cementing guild and a pedunculate guild with a functional pedicle (Alexander 1977). R-mode based analysis of similarities (ANOSIM) tested whether abundance patterns differ (1) between brachiopod and bivalve species attaining more than 5% per sample, (2) among guilds represented by more than three species (i.e., pedunculate brachiopods, epibyssate filibranchs, endobyssate filibranchs, and shallow burrowing eulamellibranchs), and (3) among groups differing in the gill type (i.e., brachiopods, protobranchs, filibranchs, pseudolamellibranchs and eulamellibranchs).

One-way analyses of similarities (ANOSIM) evaluated whether there are any differences in species and guild composition (1) among habitats differing in the wave-base level, (2) among habitats affected by different amount of siliciclastic and carbonate supply (i.e., limestones, marly limestones, and marlstones), and (3) among habitats differing in the substrate consistency (i.e., soft-bottom, mixed-bottom, and hard-bottom habitats). Well sorted grainstones and sparite-rich rudstones with signs of amalgamation indicating long-term high-energy conditions were assigned to habitats above fair-weather storm wave base (FWWB). Moderately sorted floatstones and packstones with signs of amalgamation were assigned to habitats above normal storm wave base (NSWB), implying frequent storm disturbance. Poorly sorted and loosely packed floatstones with rare storm disturbance were assigned to habitats below NSWB. Floatstones are characterized by complex internal stratification consisting of thin, non-amalgamated layers of densely-packed and moderately-sorted shell debris. Shell infillings are commonly sparitic, indicating rapid shell burial. Floatstones and wackestones with missing signs of high-energy disturbance were assigned to habitats below maximum storm wave base (MSWB). Grainstones, packstones and rudstones were assigned to hard-bottom habitats, floatstones with loosely packed shells to mixed-bottom habitats, and wackestones and floatstones with dispersed shells to soft-bottom habitats. Although these environmental assignments are affected by partial correlation, crossed testing designs that can separate effects of siliciclastic supply, wave-base level and substrate consistency are still applicable. For example, hard-bottom habitats are represented by limestones only and also represent the shallowest habitats above FWWB and NSWB only. Mixed-bottom habitats are represented by limestones and marly limestones and do not include any marlstones. Soft-bottom habitats are represented by limestones, marly limestones and marlstones.

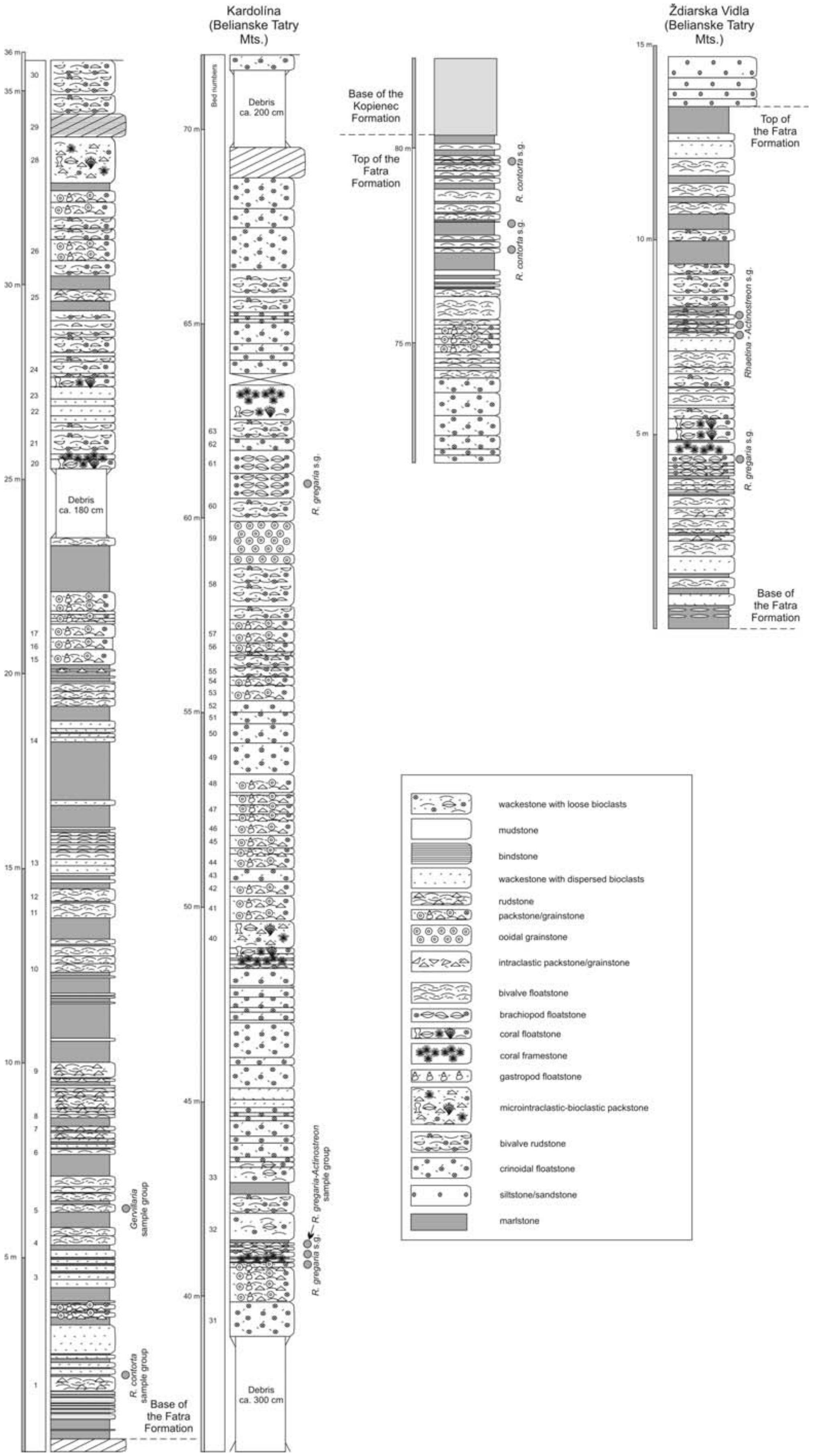


Figure 3 - The Kardolína and Ždiarska Vidla sections in the Belianske Tatry Mountains.

Discrimination of sample groups

Six sample groups sharing similar species composition and one sample unique in species composition were discriminated with Q-mode cluster analysis of 47 samples using the group-average linking method and Bray-Curtis similarity (Fig. 4). Three sample groups are dominated by epifaunal and semi-infaunal bivalves, two sample groups by brachiopods, and one sample group by cementing bivalves and brachiopods (Fig. 5-6). The sample groups are equivalent to the associations of Fürsich (1977) and community types of Bambach and Bennington (1996).

(1) The *Rhaetina gregaria-Zugmayerella* sample group is represented by five samples with 671 individuals. The sample-level richness (S) is between 5 and 11, the evenness (PIE) is between 0.5 and 0.57. This group is dominated by the pedunculate brachiopods *Rhaetina gregaria* (62.4%) and *Zugmayerella uncinata* (24.9%), followed by the less common cementing bivalves *Atreta intusstriata* (4.4%) and *Actinostreon haidingerianum* (2.7%). Other brachiopods (*Austrirhynchia cornigera, Discinisca suessi*) and bivalve species are rare (below 1%). Epibyssate (2.1%) and endobyssate bivalves (1.5%) are slightly more common than infaunal bivalves (below 1%). This group occurs in marly floatstones and marlstones, which correspond to habitats below MSWB. It is present in the lower and middle parts of the Fatra Formation (sequences 1 and 3).

(2) The *Rhaetina gregaria* sample group is one of the most common community types of the Fatra Formation, being represented by 19 samples with 2426 individuals. The sample-level richness (S) is highly variable, ranging from two to 13 species. The evenness (PIE) is low to very low (0.07-0.48). In addition to the dominant pedunculate brachiopod *R. gregaria* (83.6%), the cementing filibranch *Atreta intusstriata* is common (5.6%). Epibyssate (3.2%) and endobyssate filibranchs (1.9%) and the cementing pseudolamellibranch *Actinostreon haidingerianum* (1.5%) are less common. Shallow burrowing bivalves are rare (below 1%). This group occurs in floatstones and packstones with signs of complex internal stratification and in marly floatstones that represent habitats below NSWB and MSWB. One sample is derived from rudstone with signs of intense storm reworking (habitats above NSWB). *Rhaetina gregaria* commonly co-occurs with coral debris, with isolated colonies of branching corals (*Retiophyllia*) or is dispersed in coral thickets. With the exception of the lower part of Sequence 1, the *R. gregaria* sample group occurs in the whole Fatra Formation.

(3) The *Rhaetina gregaria-Actinostreon haidingerianum* sample group is represented by five samples with 141 individuals. Its sample-level richness varies between 3 and 5 species, the evenness (PIE) is moderately high (0.62-0.7). The pedunculate brachiopod *R. gregaria* (34.2%), the cementing pseudolamellibranch *A. haidingerianum* (31.8%), and the cementing filibranch *Atreta intusstriata* (30.9%) dominate in this sample group. *Zugmayerella uncinata* (1.2%) and epibyssate bivalves are rare. This group is limited to floatstones and floatstones/packstones, which correspond to habitats below NSWB and MSWB. It occurs in the lower and middle parts of the Fatra Formation (sequences 1 and 2).

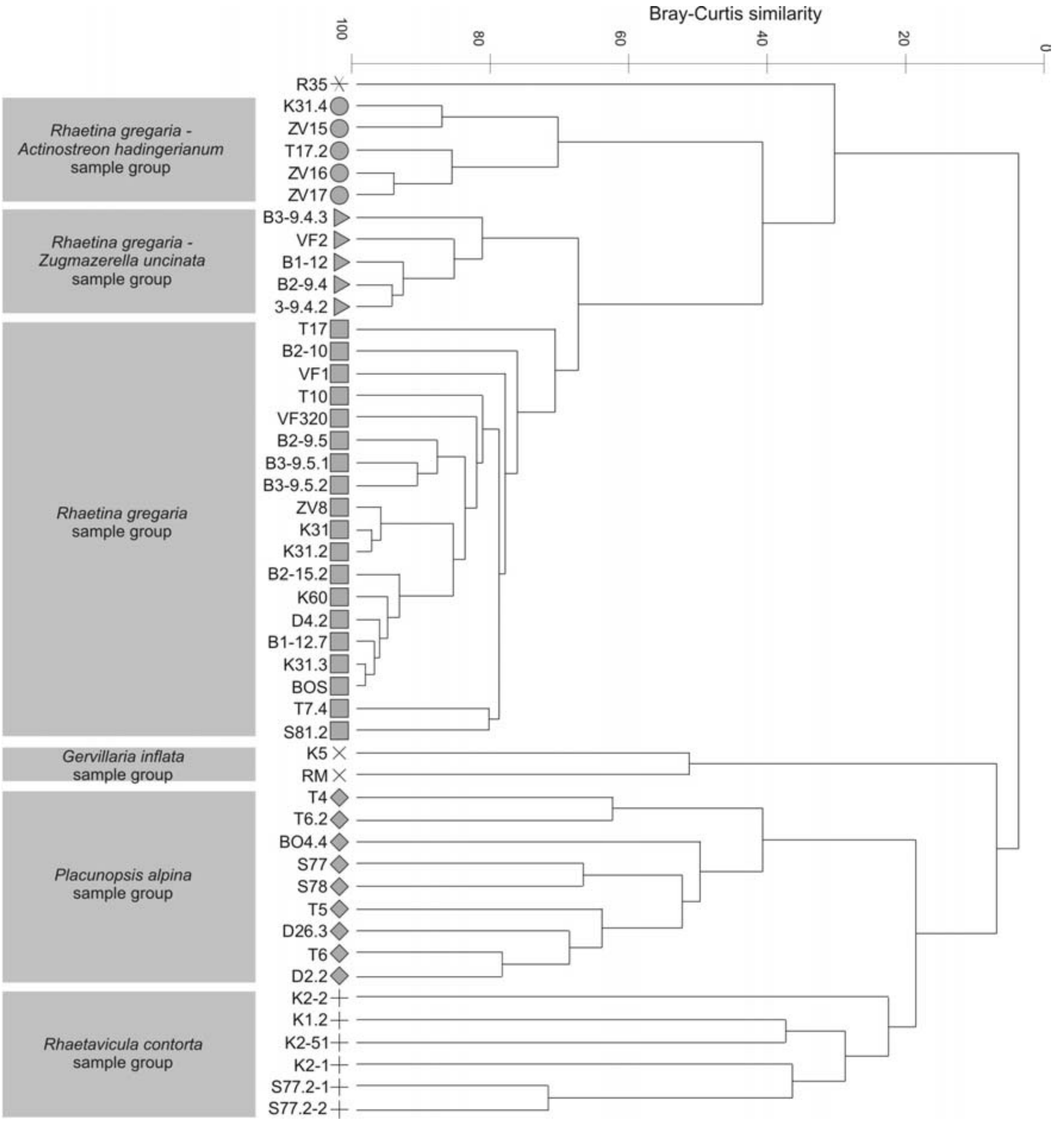


Figure 4 - Discrimination of six sample group using Q-mode cluster analysis that is based on Bray-Curtis similarity and group average linking method.

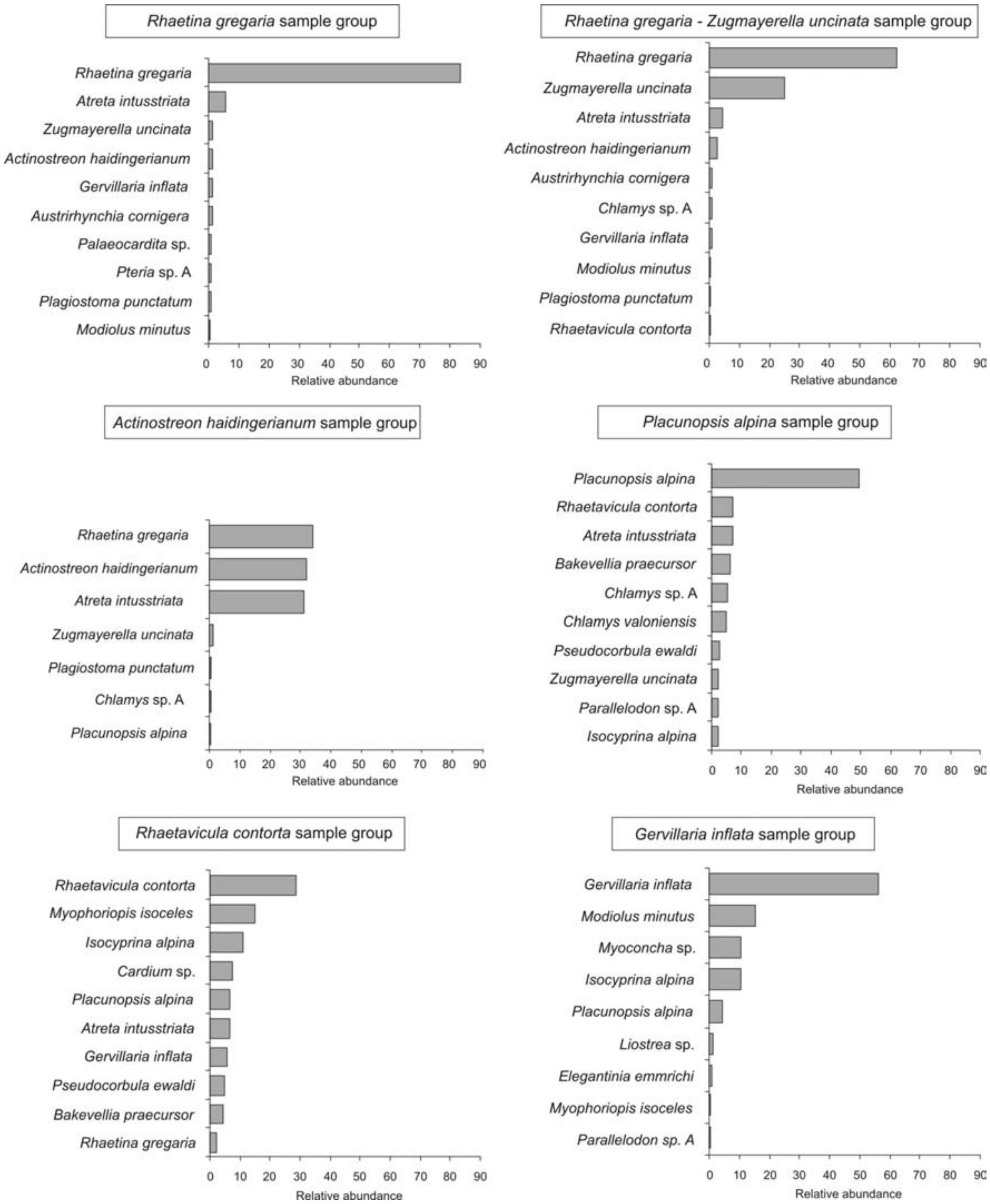


Figure 5 - Relative abundances of ten most common brachiopod and bivalve species in six sample groups.

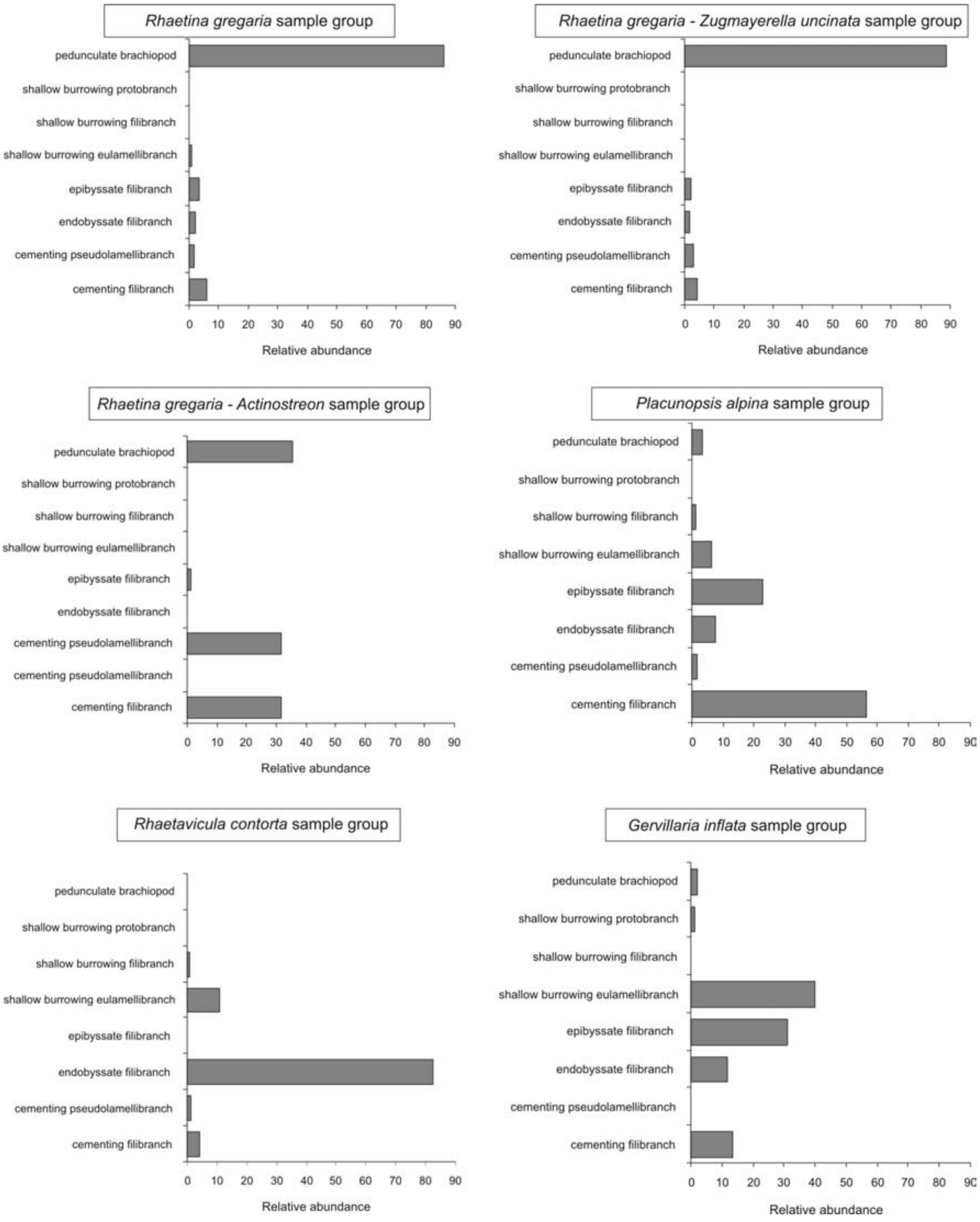


Figure 6 - Relative abundances of brachiopod and bivalve guilds in six sample groups.

(4) The *Gervillaria inflata* sample group is represented by two samples and 132 individuals. The sample-level richness (S) is between 3 and 8 species, the evenness (PIE) is moderate (0.56-0.65). It is dominated by the endobyssate filibranchs *G. inflata* (56.4%), *Modiolus minutus* (15.4%) and *Myoconcha* sp. (10.5%). Shallow burrowing (*Isocyprina alpina*, 10.5%) and cementing bivalves (*Placunopsis alpina*, 4.3%) are also common. Epibyssate bivalves are rare (0.4%) and brachiopods are absent. This group occurs in floatstones/packstones with signs of internal complex stratification (habitats above MSWB) in the lower part of Sequence 1 of the Fatra Formation.

(5) The *Rhaetavicula contorta* sample group is represented by six samples and 198 individuals. The sample-level richness (S) is between 4 and 9 species, the evenness (PIE) is moderately high (0.54-0.8). The epibyssate filibranch *R. contorta* (28.8%), and the shallow burrowing eulamellibranchs *Myophoriopis isoceles* (15%), *Isocyprina alpina* (10.8%) and *Cardium* sp. (7.5%) are abundant. The cementing filibranchs *Placunopsis alpina* (6.8%) and *Atreta intusstriata* (6.6%), and the endobyssate filibranchs *G. inflata* (6.5%) and *Bakevellia praecursor* (4.4%) are less common. *Rhaetina gregaria* is rare (2.1%). This sample group occurs in marlstones, floatstones and floatstones/packstones in the lower and upper part of the Fatra Formation (sequences 1 and 4). The deposit types correspond to habitats above NSWB and below MSWB.

(6) The *Placunopsis alpina* sample group is defined on the basis of nine samples and 727 individuals. The sample-level richness (S) varies markedly (from 3 to 15 species), the evenness (PIE) varies from 0.42 to 0.89. It is dominated by cementing (*P. alpina*, *A. intusstriata*, 56.5%) and epibyssate filibranchs (*R. contorta*, *Chlamys* sp. A, *Chlamys valoniensis, Parallelodon* sp. A, 22.8%). Endobyssate filibranchs (7.5%) and shallow burrowing eulamellibranchs (6.6%) are less common. Pedunculate brachiopods are rare (3.5%). This sample group occurs in floatstones/packstones and packstones/rudstones, representing the shallowest habitats above FWWB and above NSWB. It is present in the lower and upper part of the Fatra Formation (sequences 1 and 4).

(7) Floatstone with coral debris and 65 individuals from the upper part of the Fatra Formation (Sequence 3) is dominated by the pedunculate brachiopod *Rhaetina pyriformis* (64.3%), followed by less abundant *R. gregaria* (28.6%). Epibyssate, endobyssate and cementing bivalves are rare.

Richness and evenness of brachiopod- and bivalve-dominated samples

General comparisons. The median rarefied alpha richness for n = 30 is significantly lower in brachiopod samples with 3.8 species than in bivalve samples with 7.8 species (Wilcoxon rank sum test, p = 0.0018). The evenness of brachiopod samples is also significantly lower than that of bivalve samples (Wilcoxon rank sum test, $p < 0.0001$ for PIE and J). The median probability of interspecific encounter (PIE) is 0.36 in brachiopod samples and 0.74 in bivalve samples. The median Pielou evenness (J) is 0.44 in brachiopod samples and 0.75 in bivalve samples. The mixed sample group dominated by brachiopods and bivalves shows the median alpha richness of 4.7 species (n = 30) and the median evenness is comparable to that of bivalve samples (0.7 for PIE and 0.78 for J). Rarefied richness and PIE of samples with more than 50 individuals are shown in Figure 7. Samples of the *R. gregaria* sample groups show a high variation in species richness (Fig. 7A). With the exception of several samples from the Bystrý potok section with high species richness, they have mostly lower richness levels than the samples of the *R. gregaria-Zugmayerella* sample group of the bivalve sample groups. Two samples of the *Placunopsis alpina* sample groups are characterized by the highest richness. Similarly, sample-level variation of the *R. gregaria* sample group in PIE is high, although their PIE is mostly lower than those of the *R. gregaria-Zugmayerella* sample groups and of bivalve sample groups (Fig. 7B).

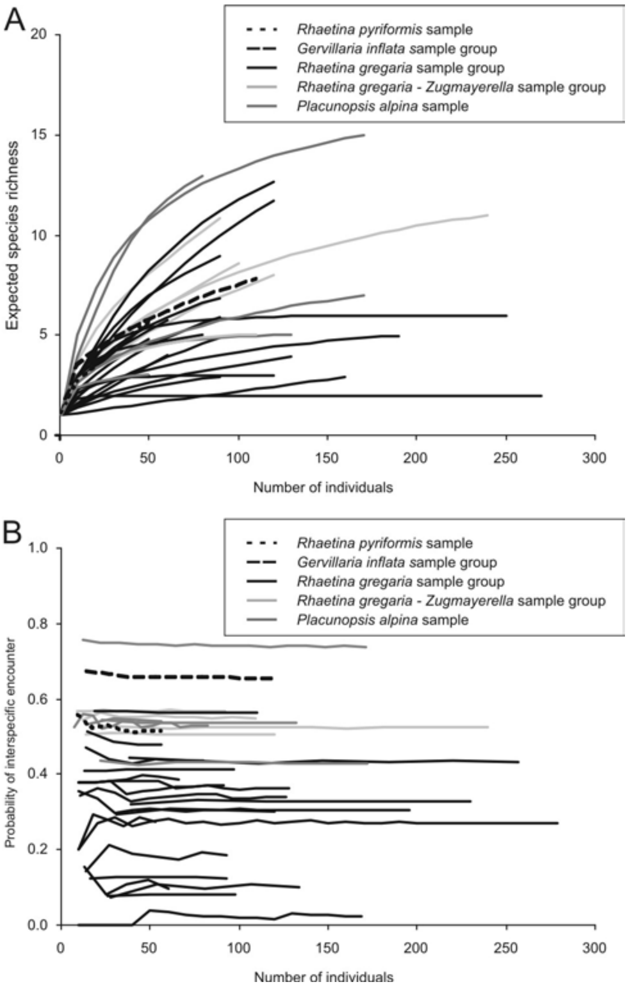


Figure 7 - A. Rarefied sample-level richness showing differences among sample groups. Only samples with more than 50 individuals are shown. B. Rarefied probability of interspecific encounter (PIE) showing differences in the evenness among sample groups. Only samples with more than 50 individuals are shown.

Between-habitat differences. Samples from four distinct habitats significantly differ in the alpha richness (Kruskal-Wallis test, H = 10.1, p = 0.017). The median alpha richness (n = 30) is higher in shallower habitats above NSWB (8.8 species in the habitats above FWWB and 6.4 species in the habitats above NSWB) than in deeper habitats below NSWB (3.9 species in the habitats below NSWB and 4 species in the habitats below MSWB). In addition, samples from four distinct habitats are also significantly different in the evenness (Kruskal-Wallis test, H = 11, p = 0.011 for PIE, H = 9.3, p = 0.025 for J). The median PIE is higher in shallower habitats above NSWB (0.74 in the habitats above FWWB and 0.66 in the habitats above NSWB) than in deeper habitats below NSWB (0.39 in the habitats below NSWB and 0.51 in the habitats below MSWB). With respect to the siliciclastic supply the differences in evenness are significant between limestones, marly limestones and marlstones (Kruskal-Wallis test, H = 12, p = 0.0025 for PIE, H = 8.52, p = 0.014 for J). Limestones (PIE = 0.65) show the higher median evenness than marly limestones (PIE = 0.34) and marlstones (PIE = 0.55). The differences in the alpha species richness (n = 30) are rather low and insignificant. There are also differences in species richness and evenness among three deposit types with distinct packing (Kruskal-Wallis test, H = 8.82, p = 0.012 for richness, H = 6.5, p = 0.039 for PIE, H = 5.95, p = 0.05 for J). The expected median alpha richness of floatstones (4 species) and floatstones/packstones (4.1 species) is lower than that of packstones/rudstones (8.5 species). In addition, the evenness of floatstones (PIE = 0.38, J = 0.45) and floatstones/packstones (PIE = 0.51, J = 0.62) is lower than that of packstones/rudstones (PIE = 0.64, J = 0.65).

Sample	Sample group	S	N	ES(30)	PIE	Pielou J'	H'(loge)
K5	*Gervillaria inflata*	8	119	4.78	0.65	0.62	1.28
T4	*Placunopsis alpina*	12	37	11.43	0.90	0.91	2.26
T5	*Placunopsis alpina*	15	171	8.84	0.74	0.69	1.87
T6	*Placunopsis alpina*	13	82	8.20	0.53	0.54	1.39
T6.2	*Placunopsis alpina*	11	45	9.98	0.85	0.86	2.07
D2.2	*Placunopsis alpina*	7	172	3.85	0.43	0.44	0.85
D26.3	*Placunopsis alpina*	5	132	3.90	0.54	0.61	0.98
BO4.4	*Placunopsis alpina*	3	56	2.79	0.54	0.75	0.82
K2-2	*Rhaetavicula contorta*	9	40	7.99	0.76	0.77	1.70
S77.2-1	*Rhaetavicula contorta*	9	42	7.83	0.78	0.78	1.72
S77.2-2	*Rhaetavicula contorta*	8	41	7.33	0.80	0.83	1.73
K31.4	*R. gregaria - A. haidingerianum*	5	33	4.82	0.70	0.78	1.26
ZV16	*R. gregaria - A. haidingerianum*	4	30	4.00	0.69	0.84	1.17
ZV17	*R. gregaria - A. haidingerianum*	5	35	4.71	0.70	0.78	1.26
B9.5	*Rhaetina gregaria*	13	128	5.96	0.36	0.38	0.98
B9.5.1	*Rhaetina gregaria*	5	53	3.69	0.27	0.36	0.59
B9.5.2	*Rhaetina gregaria*	12	126	5.05	0.34	0.35	0.87
B10	*Rhaetina gregaria*	7	97	4.34	0.41	0.44	0.86
B15.2	*Rhaetina gregaria*	6	93	3.36	0.18	0.26	0.46
B12.7	*Rhaetina gregaria*	4	60	2.50	0.10	0.18	0.25
D4.2	*Rhaetina gregaria*	3	169	1.36	0.02	0.07	0.07
T7.4	*Rhaetina gregaria*	6	66	4.21	0.39	0.45	0.80
T10	*Rhaetina gregaria*	9	91	5.40	0.37	0.41	0.91
T17	*Rhaetina gregaria*	3	56	2.79	0.48	0.69	0.75
K31a	*Rhaetina gregaria*	2	279	2.00	0.27	0.64	0.44
K31.2	*Rhaetina gregaria*	5	196	2.83	0.30	0.36	0.58
K31.3	*Rhaetina gregaria*	3	98	1.98	0.08	0.18	0.19
K60	*Rhaetina gregaria*	5	93	2.66	0.12	0.20	0.32
S81.1	*Rhaetina gregaria*	6	257	4.74	0.43	0.53	0.95
VF320	*Rhaetina gregaria*	5	230	3.15	0.33	0.40	0.64
VF1	*Rhaetina gregaria*	5	80	4.19	0.44	0.55	0.89
ZV8	*Rhaetina gregaria*	3	120	2.76	0.30	0.51	0.56
BOS	*Rhaetina gregaria*	4	134	2.17	0.10	0.18	0.25
B9.4	*R. gregaria - Z. uncinata*	9	109	4.66	0.55	0.49	1.08
B12	*R. gregaria - Z. uncinata*	11	240	4.78	0.52	0.46	1.10
B9.4.2	*R. gregaria - Z. uncinata*	8	120	4.02	0.50	0.46	0.96
B9.4.3	*R. gregaria - Z. uncinata*	11	92	6.37	0.57	0.55	1.31
VF2	*R. gregaria - Z. uncinata*	5	110	3.81	0.56	0.62	0.99
R35	*R. pyriformis*	6	56	4.14	0.51	0.52	0.93

Table 1 - Summary of sample-level richness and evenness of 39 samples that have more than 30 individuals. Explanations: S – number of species, N – number of individuals, PIE – Probability of interspecific encounter, Pielou J – Pielou´s evenness index, H´($\log_e$) – Shannon-Wiener diversity index.

Within-habitat differences. To exclude the effects of habitat differences on richness and evenness of brachiopod and bivalve samples, their diversity should be compared within relatively uniform habitat conditions. However, such comparisons are limited to those habitats where both brachiopod and bivalve samples are represented by more than one sample. The mixed sample group was not included in the comparisons. With respect to siliciclastic supply, the differences in the alpha richness between brachiopod and bivalves samples in limestones are insignificant (Wilcoxon rank sum test, p = 0.1). In contrast, bivalve samples have significantly higher evenness than brachiopod samples (Wilcoxon rank sum test, p = 0.006 for PIE, p = 0.009 for J). With respect to sediment packing, brachiopod and bivalve samples do not differ in their expected richness in floatstones/packstones (Wilcoxon rank sum test, p = 0.12). Bivalve samples have significantly higher PIE than brachiopod samples, although the differences in J are insignificant (Wilcoxon rank sum test, p = 0.036 for PIE, p = 0.14 for J).

Compositional differences among brachiopod- and bivalve-dominated samples

Species abundance. The samples dominated by brachiopods and bivalves are completely segregated in NMDS, implying that brachiopods and bivalves display abundance patterns shared among their constituent species (Fig. 8A). The mixed sample group dominated by *Rhaetina gregaria* and *Actinostreon haidingerianum* is more similar to brachiopod than to bivalve samples. Brachiopod and bivalve samples are segregated along the first axis in DCA (Fig. 8B). Based on abundances of bivalve species only (Fig. 8E), brachiopod and bivalves samples show little compositional overlap, implying that some bivalve species had differential abundances between brachiopod and bivalve samples. The mixed sample group is compositionally similar to brachiopod samples in terms of bivalve species abundances. For example, *Atreta intusstriata, Actinostreon haidingerianum* and *Plagiostoma punctatum* are more common in brachiopod than in bivalve samples. Brachiopod and bivalve-dominated samples thus also differ in their taxonomic structure with respect to abundances of bivalves alone.

Guild abundance. The samples dominated by brachiopods and bivalves are compositionally segregated in Q-mode NMDS based guild abundances (Fig. 8C). In DCA, brachiopod and bivalve samples are segregated along the first axis (Fig. 8D). Brachiopod samples are compositionally more similar to the *Placunopsis alpina* sample group than to other bivalve sample groups. Pedunculate brachiopods can occur in this sample group and cementing filibranchs are common in brachiopod samples and in the *Placunopsis alpina* sample group. Cementing bivalves dominate in the mixed sample group. Epibyssate, endobyssate and shallow burrowing bivalves are invariably more common in bivalve than in brachiopod samples. Based on abundances of bivalve guilds only, brachiopod and bivalve samples show a large compositional overlap in Q-mode NMDS (Fig. 8F). This similarity is mainly caused by similar abundances of epibyssate, endobyssate and cementing filibranchs in both groups. For example, *Atreta intusstriata* is common in brachiopod samples and *Placunopsis alpina* in bivalve samples. Although samples dominated by infaunal bivalves do not overlap with brachiopod samples, brachiopod samples do not consistently differ from samples dominated by epifaunal bivalves in terms of bivalve guild abundances.

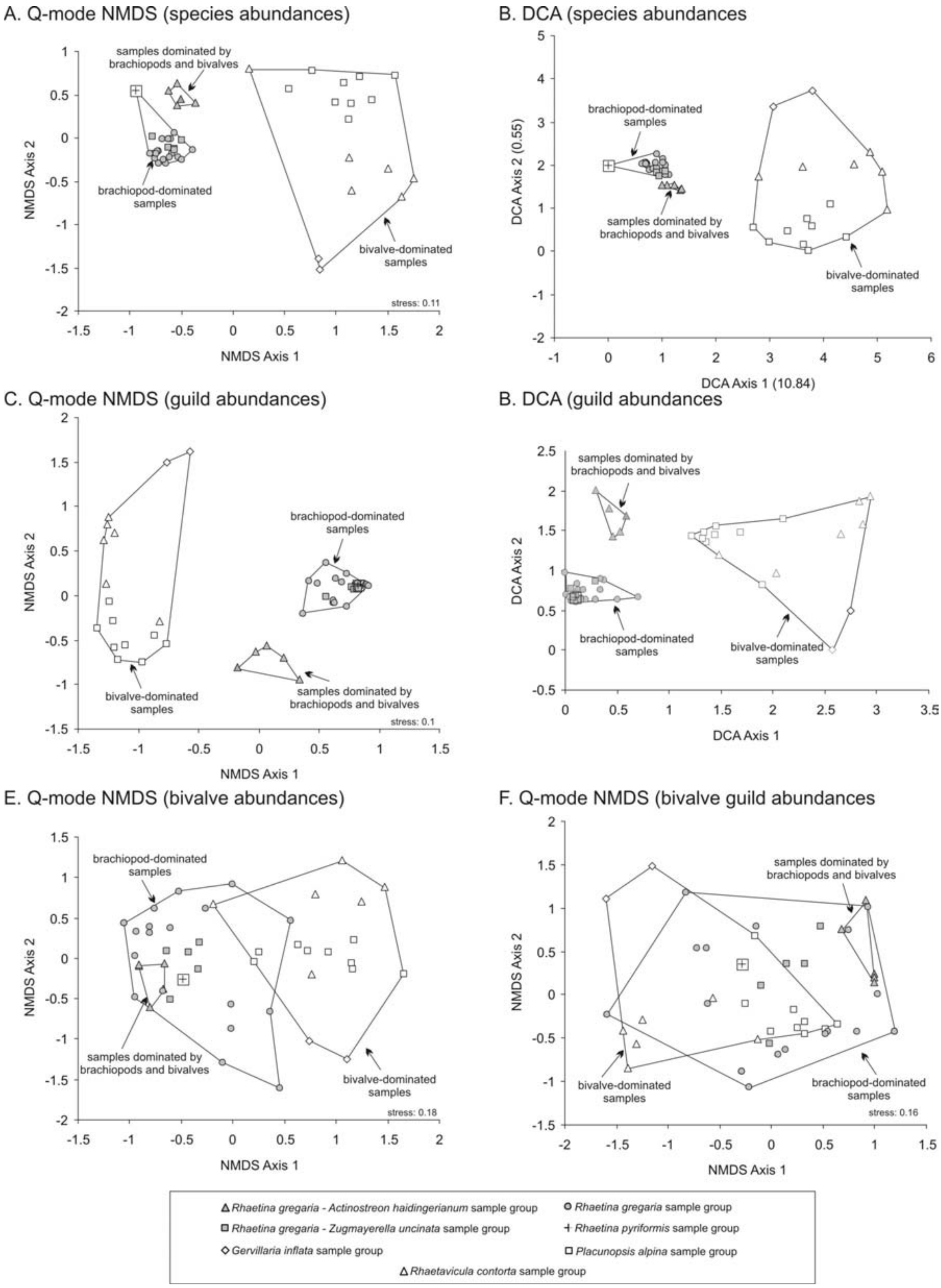


Figure 8 - Comparison of compositional relationship among samples dominated by brachiopods and bivalves in ordination plots. A. Q-mode non-metric multidimensional scaling (NMDS) based on species abundances. B. Ordination of samples in detrended correspondence analysis (DCA) based on species abundances. C. Q-mode NMDS based on guild abundances. D. Ordination of samples in detrended correspondence analysis (DCA) based on guild abundances. E. Q-mode NMDS based on abundances of bivalve species. F. Q-mode NMDS based on abundances of bivalve guilds.

Co-occurrence patterns of brachiopods and bivalves

R-mode NMDS based on species abundances (Fig. 9A) shows a partial separation between brachiopod and bivalve species in terms of their abundances. The difference in species abundances between brachiopods and bivalves is relatively low but significant using R-mode based ANOSIM ($R = 0.27$, $p = 0.043$; Tab. 2). DCA based on species abundances shows that brachiopods are characterized by the lowest species scores and eulamellibranch bivalves by the highest species scores along the first axis (Fig. 9B). Filibranchs show wide range of species scores along the first axis but are mostly well segregated from brachiopods. R-mode NMDS based on guild abundances (Fig. 9C) and Bray-Curtis similarities (Tab. 3) indicate that pedunculate brachiopods co-occurred more commonly with cementing, free-lying and epibyssate bivalves than with shallow burrowing bivalves. To test the differences among abundances of guilds, only four guilds represented by more than three species were evaluated with R-mode based ANOSIM. To simplify the comparison, guilds subdivided according to the feeding strategies were also compared separately (i.e., brachiopods with lophophores, protobranchs, filibranchs, pseudolamellibranchs, and eulamellibranchs).

There are significant differences in species abundances among pedunculate brachiopods, epibyssate and endobyssate filibranchs, and shallow burrowing eulamellibranchs ($R = 0.36$, $p < 0.0001$). As follows from pairwise between-guild comparisons, pedunculate brachiopods significantly differ in sample-level relative abundance from epibyssate filibranchs ($R = 0.63$, $p = 0.003$) and shallow burrowing eulamellibranchs ($R = 0.45$, $p = 0.0095$). The differences between epibyssate filibranchs and shallow burrowing eulamellibranchs ($R = 0.42$, $p = 0.0023$), and between epibyssate and endobyssate filibranchs ($R = 0.39$, $p = 0.0038$) are also moderately high and significant.

There are also significant differences among groups differing in the gill type ($R = 0.35$, $p = 0.0009$). The difference between pseudolamellibranchs and eulamellibranch bivalves is moderately high ($R = 0.51$, $p = 0.034$). The difference between brachiopods and eulamellibranch bivalves is relatively high and significant ($R = 0.45$, $p = 0.0095$). Filibranchs also differed in abundance patterns from brachiopods ($R = 0.39$, $p = 0.018$) and eulamellibranch bivalves ($R = 0.29$, $p = 0.012$). In terms of Bray-Curtis similarities, eulamellibranchs co-occurred rarely with brachiopods ($BC = 5.7$) and pseudolamellibranchs ($BC = 3.4$). In contrats, Bray-Curtis similarities between brachiopods and filibranchs ($BC = 23.4$), and between brachiopods and pseudolamellibranchs were higher ($BC = 26.3$).

Compositional differences among sequences

Testing the differences among four stratigraphic sequences that are bounded by unconformities shows that there are no consistent temporal variations in species and guild composition (Tab. 4). However, samples from sequences 2 and 3 contain brachiopod and mixed sample groups only. To decrease this effect of unbalanced sampling, testing of temporal turnover was restricted to non-bivalve sample groups, but the differences in species and guild composition are also low and insignificant (Tab. 4). The differences among stratigraphic sequences are also minimal and insignificant when siliciclastic supply ($R = 0.032$, $p = 0.36$) and substrate ($R = 0.12$, $p = 0.052$) are kept constant. When habitat is kept constant, the differences among stratigraphic sequences are low although significant ($R = 0.114$, $p = 0.038$).

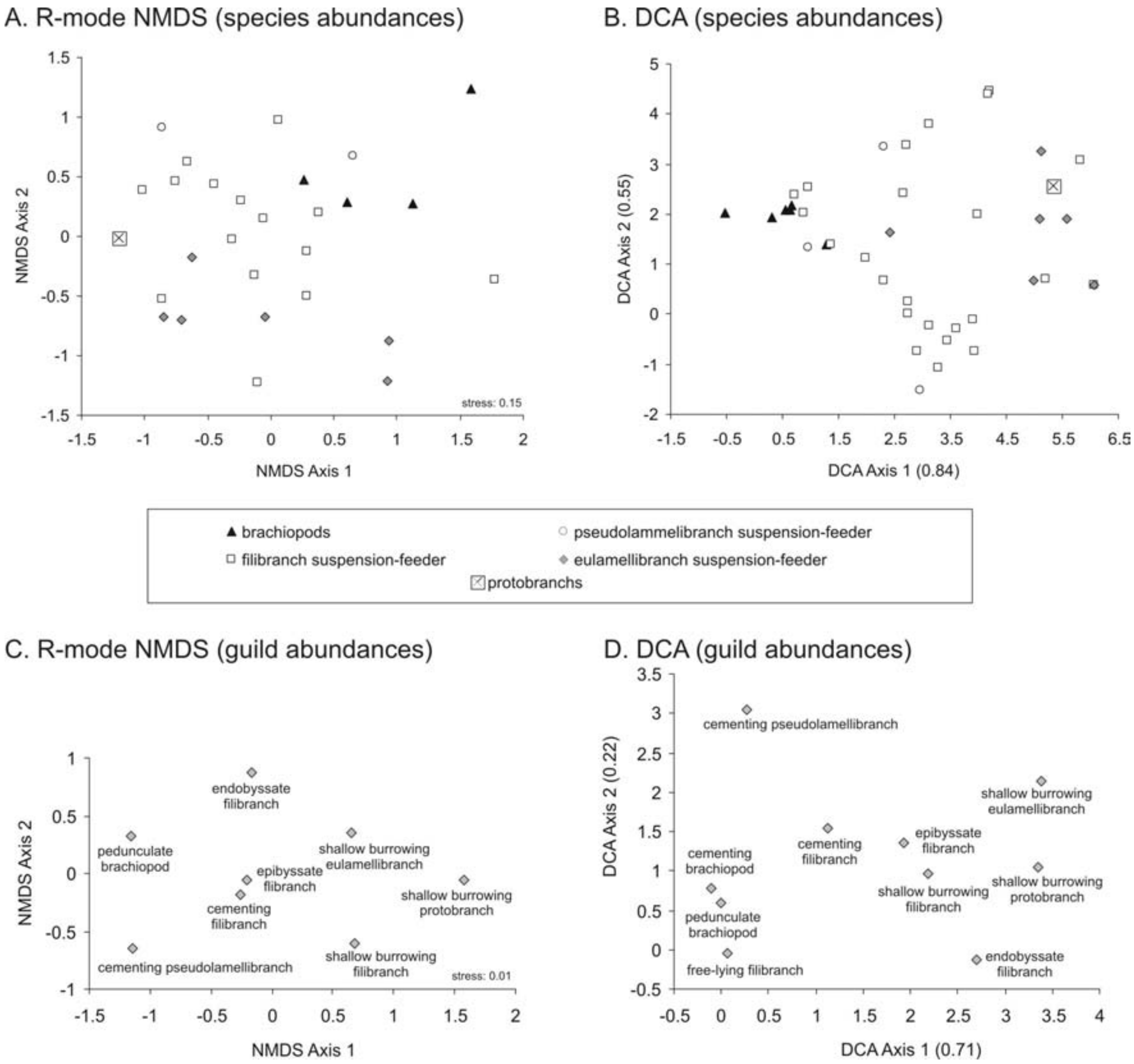


Figure 9 - Exploratory analyses of co-occurrence patterns of brachiopods and bivalves. A. R-mode non-metric multidimensional scaling (NMDS) based on species abundances. B. Ordination of species in detrended correspondence analysis (DCA) based on species abundances. C. R-mode NMDS based on guild abundances. D. Ordination of guilds in detrended correspondence analysis (DCA) based on guild abundances.

	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Bivalve species vs. brachiopod species	0.267	0.043	10000	426
Guilds with more than three species				
Global test	0.359	<0.0001	10000	0
pedunculate vs. epibyssate	0.627	0.003	330	1
pedunculate vs. endobyssate	0.094	0.21	126	27
pedunculate vs. eulamellibranch shallow burrower	0.448	0.0095	210	2
epibyssate vs. endobyssate	0.386	0.0038	792	3
epibyssate vs. eulamellibranch shallow burrower	0.418	0.0023	1716	4
endobyssate vs. eulamellibranch shallow burrower	0.056	0.3	462	139
Feeding strategies				
Global test	0.346	0.0009	10000	9
brachiopods vs. filibranch bivalves	0.386	0.018	3876	71
brachiopods vs. pseudolammelibranch bivalves	0.321	0.13	15	2
brachiopods vs. eulamellibranch bivalves	0.448	0.0095	210	2
filibranch vs. pseudolammelibranch bivalves	0.214	18	136	25
filibranch vs. eulamellibranch bivalves	0.288	0.0118	10000	118
pseudolammelibranch vs. eulamellibranch bivalves	0.51	0.0357	28	1

Table 2 - Analysis of similarities (ANOSIM) showing differences in species abundance among brachiopods and bivalves. The alpha value for the pairwise comparisons was is lowered by the Bonferroni correction to 0.0083 (0.05/6).

Pairwise comparisons - feeding strategies	BC similarity
protobranch vs. lophophorate	0.3
filibranch vs. lophophorate	23.4
pseudolammelibranch vs. lophophorate	26.3
eulamellibranch vs. lophophorate	5.7
filibranch vs. protobranch	7.6
pseudolammelibranch vs. protobranch	0.0
eulamellibranch vs. protobranch	15.8
pseudolammelibranch vs. filibranch	23.6
eulamellibranch vs. filibranch	27.1
eulamellibranch vs. pseudolamellibranch	3.4

Table 3 – Bray-Curtis similarities between guilds differing in the gill type.

Compositional differences within sequences

Evaluating whether community composition varies within sequences was restricted to Sequence 1 because it is relatively well sampled with respect to its stratigraphic range. Substantial within-sequence temporal turnover is indicated by replacement of bivalve by brachiopod sample groups in its middle part. This part is marked by an abrupt replacement of grainstones and rudstones by floatstones that corresponds to the substitution of shoreline progradation by rapid retrogradation of shallow-water sediments. The difference in species and guild composition between the progradation and retrogradation part of Sequence 1 is striking (Fig. 13; R [species] = 0.796, $p < 0.0001$, R [guilds] = 0.768, $p < 0.0001$ for guilds). This difference is also very high when siliciclastic supply is kept constant (R [species] = 0.76, $p < 0.0001$; R [guilds] = 0.68, p = 0.0001), when wave-base level is kept constant (R = [species] = 0.85, p = 0.0001; R [guilds] = 0.87, p = 0.0004), and also when substrate consistency is kept constant (R [species] = 0.9, $p < 0.0001$; R [guilds] = 0.84, $p < 0.0001$). It means that distribution patterns along an onshore-offshore gradient completely changed during deposition of sequences.

During the progradational phase of Sequence 1, onshore-offshore gradient was dominated by cementing, epibyssate and endobyssate filibranchs and shallow burrowing eulamellibranchs in all habitats above MSWB (Figs. 11-12). Pedunculate brachiopods were rare. The compositional separation among the habitats above FWWB, above NSWB and below NSWB (Fig. 10) is relatively low but significant for species abundances (R = 0.27, p = 0.027) and insignificant for guild abundances (R = 0.16, p = 0.1). Note that brachiopod-dominated communities did not occur along the onshore-offshore gradient during this time interval.

During the retrogradational phase of Sequence 1, onshore-offshore gradient was dominated by pedunculate brachiopods. In contrast to the progradational phase, there were no bivalve-dominated communities and between-habitat differences in the species and guild abundances were low. The compositional separation among habitats above NSWB, below NSWB and below MSWB (Fig. 10) was very low and insignificant both for species and guild abundances (R = 0.26, p = 0.06 for species, R = 0.18, p = 0.09 for guilds)). Although data are not available from the shallowest habitats above FWWB, brachiopods were dominant both in shallow and deep habitats (Figs. 11-12). In addition to the replacement of bivalve- by brachiopod-dominated communities, new taxa in the upper part of Sequence 1 include also red algae, sponges and branching and platy corals, locally forming dense coral thickets.

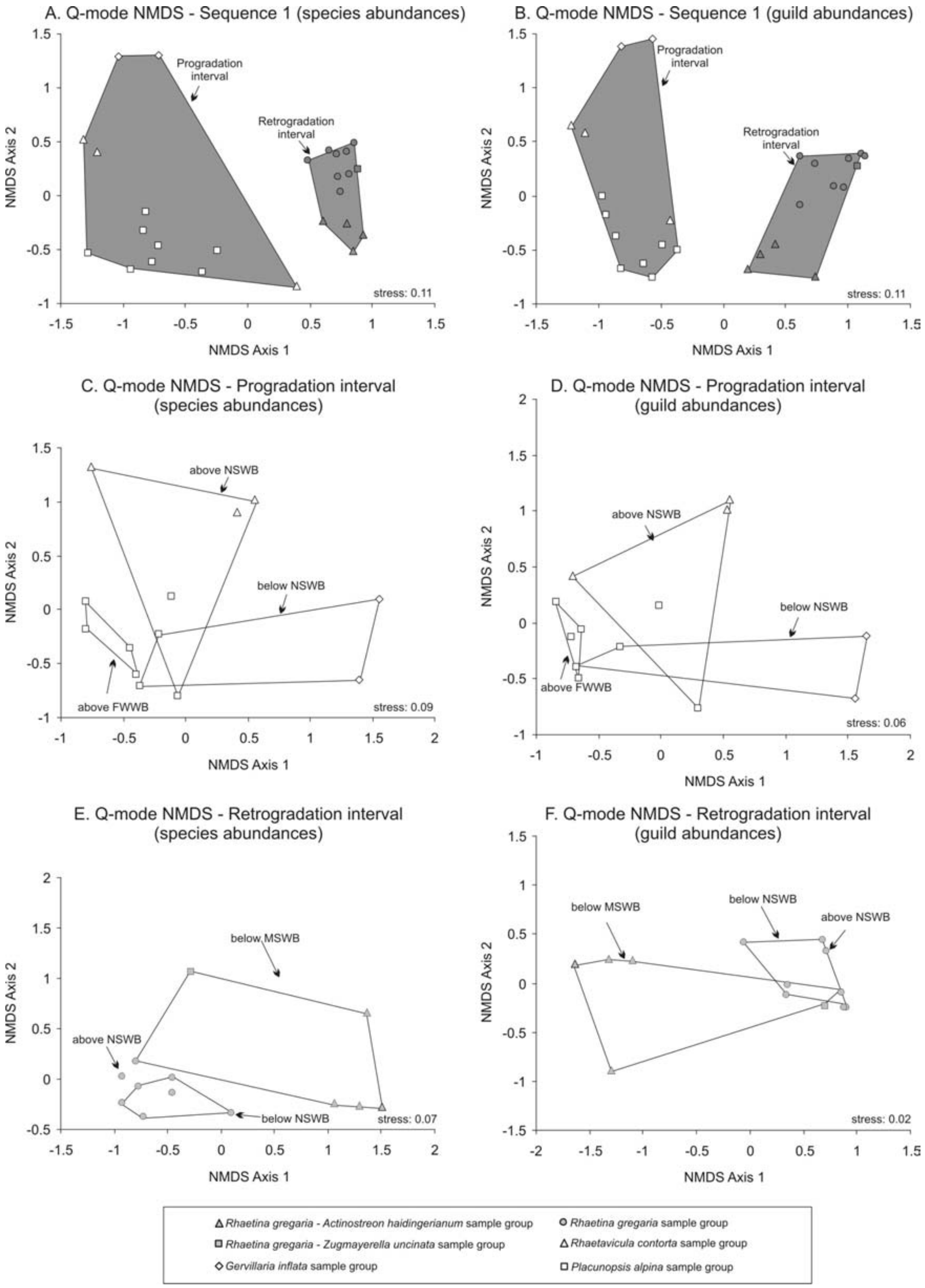


Figure 10 - A. Q-mode NMDS showing differences in species composition between the progradational and retrogradational intervals within Sequence 1. B. Q-mode NMDS showing differences in guild composition between the progradational and retrogradational intervals within Sequence 1. C. Between-habitat differences in NMDS based on species abundances in the progradational part of Sequence 1. D. Between-habitat differences in NMDS based on species abundances in the retrogradational part of Sequence 1. E. Between-habitat differences in NMDS based on guild abundances in the progradational part of Sequence 1. F. Between-habitat differences in NMDS based on guild abundances in the retrogradational part of Sequence 1.

	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Species - stratigraphic sequences				
Global test	0.039	0.261	10000	2610
Guilds - stratigraphic sequences				
Global test	0.086	0.106	10000	1058
Species - progradational vs. retrogradational part of Sequence 1				
Global test	0.796	<0.0001	10000	0
Guilds - progradational vs. retrogradational part of Sequence 1				
Global test	0.768	<0.0001	10000	0

Table 4 - Analysis of similarities (ANOSIM) showing differences in species abundance and guild abundances among four stratigraphic sequences and between the progradational and retrogradational part of Sequence 1.

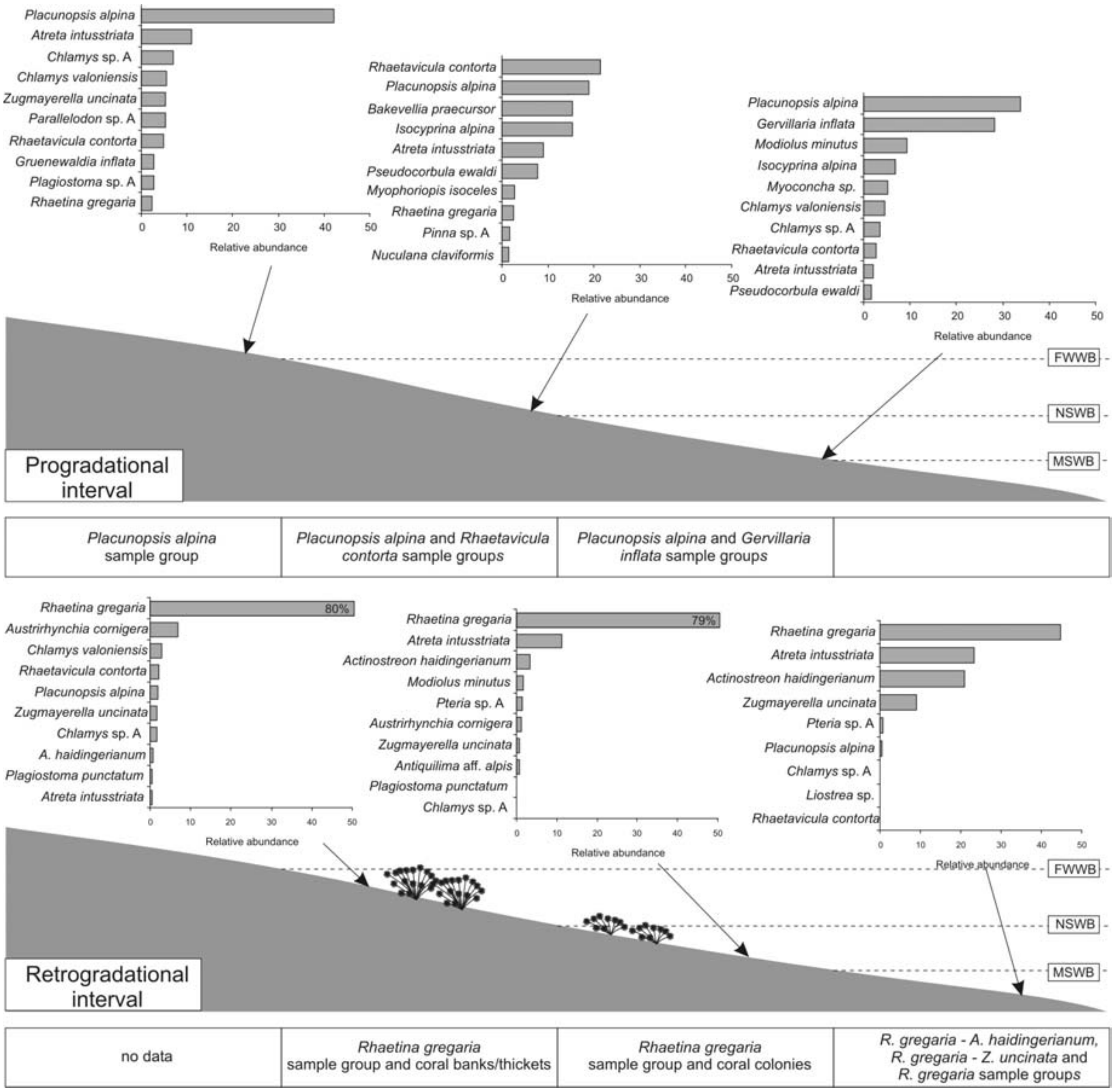


Figure 11 - Distribution patterns of brachiopod and bivalve species along an onshore-offshore gradient during the progradational and retrogradational intervals of Sequence 1.

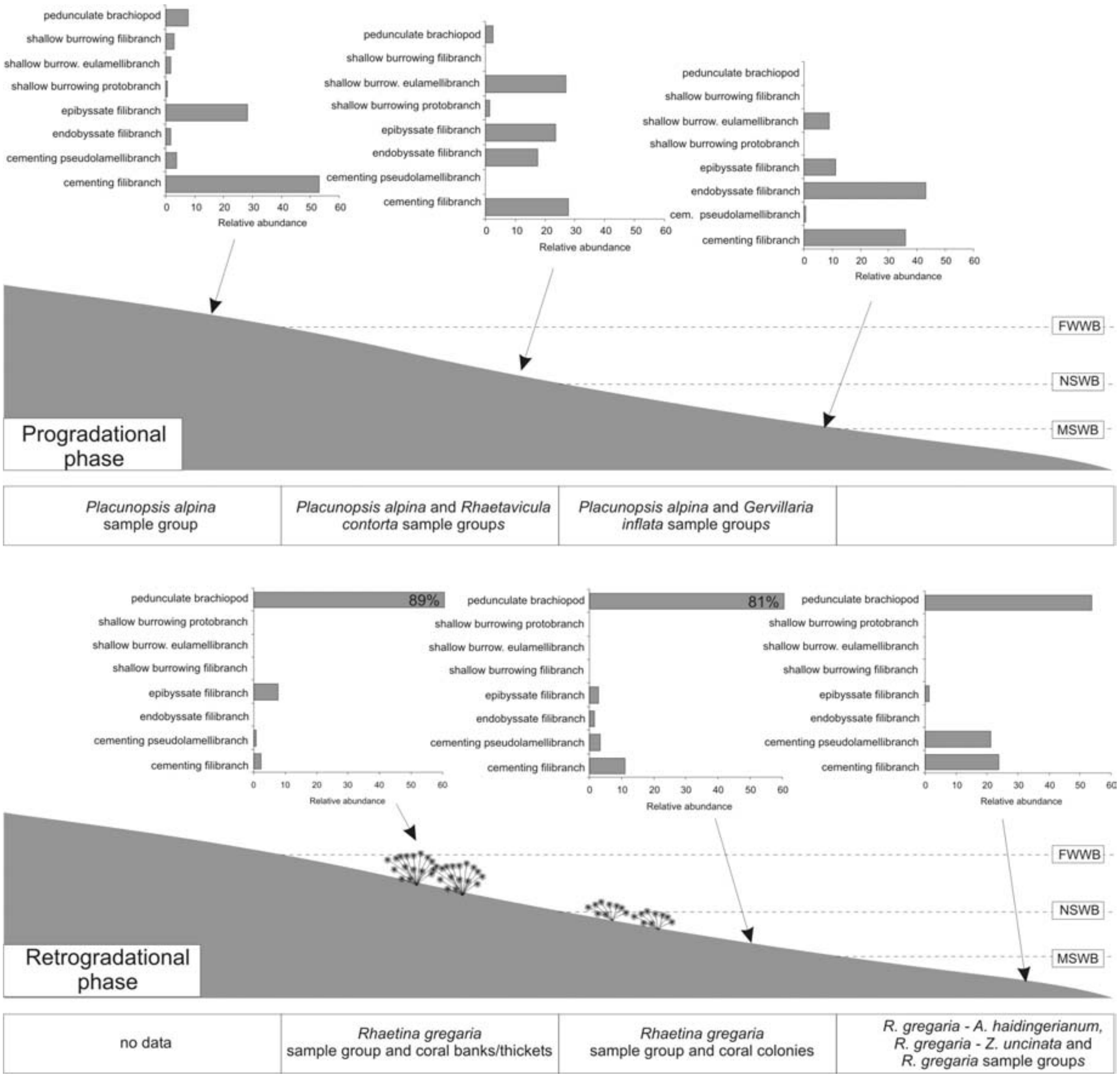


Figure 12 - Distribution patterns of brachiopod and bivalve guilds along an onshore-offshore gradient during the progradational and retrogradational intervals of Sequence 1.

Effects of siliciclastic supply

One-way analyses. One-way ANOSIM shows that the compositional differences among limestones, marly limestones and marlstones are significant both for species (R = 0.263, p = 0.0002) and guilds (R = 0.265, p < 0.0001). Pairwise differences are significant between marly limestones and marlstones and between marly limestones and limestones (Tab. 5). However, the difference between end-member marlstones and limestones is insignificant both for species and guilds. Abundance plots indicate that the response of species and guilds was not monotonic with respect to increasing siliciclastic supply. Marly limestones were characterized by the highest abundance of pedunculate brachiopods (*R. gregaria*; Fig. 13). Marlstones were also dominated by pedunculate brachiopods, but shallow burrowing eulamellibranchs and epibyssate and cementing filibranchs were also common. Limestones were dominated by cementing filibranchs (*Placunopsis alpina* and *Atreta intusstriata*), followed by pedunculate brachiopods and epibyssate and endobyssate filibranchs. High abundance of both infaunal bivalves and brachiopods in marlstones, however, follows from pooling of samples strongly differing in their composition. Brachiopods and infaunal bivalves were rarely abundant together in one sample.

One-way ANOSIM	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Species - siliciclastics vs. carbonates				
Global test	0.263	0.0002	10000	2
Marlstone vs. marly limestone	0.485	0.001	10000	12
Marlstone vs. limestone	0.029	0.301	10000	3010
Marly limestone vs. limestone	0.302	<0.0001	10000	0
Guilds - siliciclastics vs. carbonates				
Global test	0.265	<0.0001	10000	0
Marlstone vs. marly limestone	0.262	0.024	10000	237
Marlstone vs. limestone	0.046	0.228	10000	2281
Marly limestone vs. limestone	0.354	<0.0001	10000	0

Two-way ANOSIM (siliciclastic effects, allowing for habitat effects)	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Species - siliciclastics vs. carbonates				
Global test	0.23	0.0014	10000	14
Marlstone vs. marly limestone	0.203	0.024	6435	153
Marlstone vs. limestone	0.099	0.26	720	187
Marly limestone vs. limestone	0.312	0.0014	10000	14
Guilds - siliciclastics vs. carbonates				
Global test	0.21	0.035	10000	35
Marlstone vs. marly limestone	0.058	0.17	6435	1116
Marlstone vs. limestone	-0.038	0.48	720	351
Marly limestone vs. limestone	0.37	0.0008	10000	8

Two-way ANOSIM (siliciclastic effects, allowing for substrate effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - siliciclastics vs. carbonates				
Global test	0.44	<0.0001	10000	0
Marlstone vs. marly limestone	0.514	0.0002	10000	2
Marlstone vs. limestone	0.017	0.31	1287	394
Marly limestone vs. limestone	0.538	0.0002	10000	2
Guilds - siliciclastics vs. carbonates				
Global test	0.298	0.0016	10000	16
Marlstone vs. marly limestone	0.217	0.031	10000	313
Marlstone vs. limestone	0.01	0.34	1287	447
Marly limestone vs. limestone	0.511	0.0003	10000	3

Table 5 - Analysis of similarities (ANOSIM) showing differences in species abundance and guild abundances among habitats differing in the siliciclastic supply. Effects of siliciclastic supply are tested with (1) one-way analyses that do not take into account effects of other factors, (2) two-way crossed analyses that keep wave-base level constant, and (3) two-way crossed analyses that keep substrate consistency constant. The p-value in bold indicate the differences that are significant. Applying the Bonferroni correction lowers the alpha value for pairwise comparisons to 0.017 (0.05/3).

Separation of wave-base level effects. Two-way crossed ANOSIM tests whether there are any differences among habitats differing in the siliciclastic supply, allowing for differences with respect to wave-base level. When wave-base level is kept constant, there are significant differences among marlstones, marly limestones and limestones in species ($R = 0.23$, $p = 0.0014$) and guild composition ($R = 0.21$, $p = 0.035$). Because substrate types co-vary with wave-base level differences, the differences among marlstones, marly limestone and limestones were further restricted to soft-bottom and mixed-bottom habitats. In soft-bottom habitats, there are moderate and significant differences in species (R = 0.35, p = 0.0036) and guild composition (R = 0.27, p = 0.0125) among habitats with constant wave-base level but differing in the siliciclastic supply. In mixed-bottom habitats, the differences among habitats differing in the siliciclastic supply are insignificant for species (R = -0.08, p = 0.64) and guild composition (R = -0.17, p = 0.85).

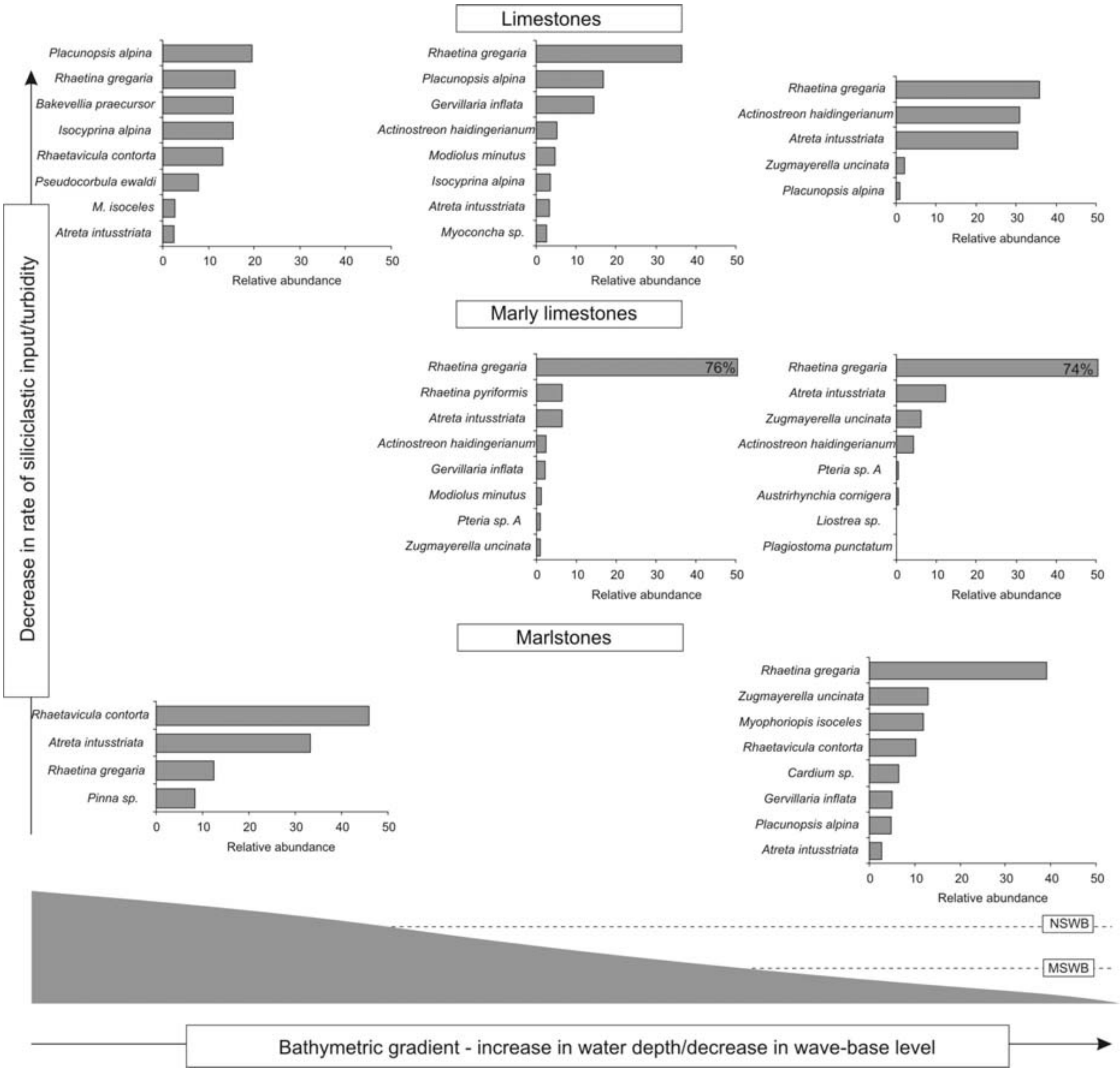


Figure 13 - Distribution of brachiopod and bivalve species along a gradient with varying siliciclastic supply and varying wave-base level.

Separation of substrate effects. In this case, two-way crossed ANOSIM tests whether there are any differences among habitats differing in the siliciclastic supply, allowing for differences with respect to substrate consistency. When substrate properties are kept constant, there are significant differences among marlstones, marly limestones and limestones in species (R = 0.44, p < 0.0001) and guild composition (R = 0.3, p = 0.0016). Because substrate types co-vary with wave-base level differences, the differences among marlstones, marly limestone and limestones were further restricted to habitats below MSWB and to habitat below NSWB. In habitats below MSWB, there are moderate and significant differences in species (R = 0.31, p = 0.0059) and guild composition (R = 0.21, p =

0.038) among habitats with constant substrate types but differing in the siliciclastic supply. However, in habitats below NSWB, the differences among habitats with constant substrate types but differing in the siliciclastic supply are insignificant for species (R = 0.22, p = 0.13) and guild composition (R = 0.18, p = 0.18).

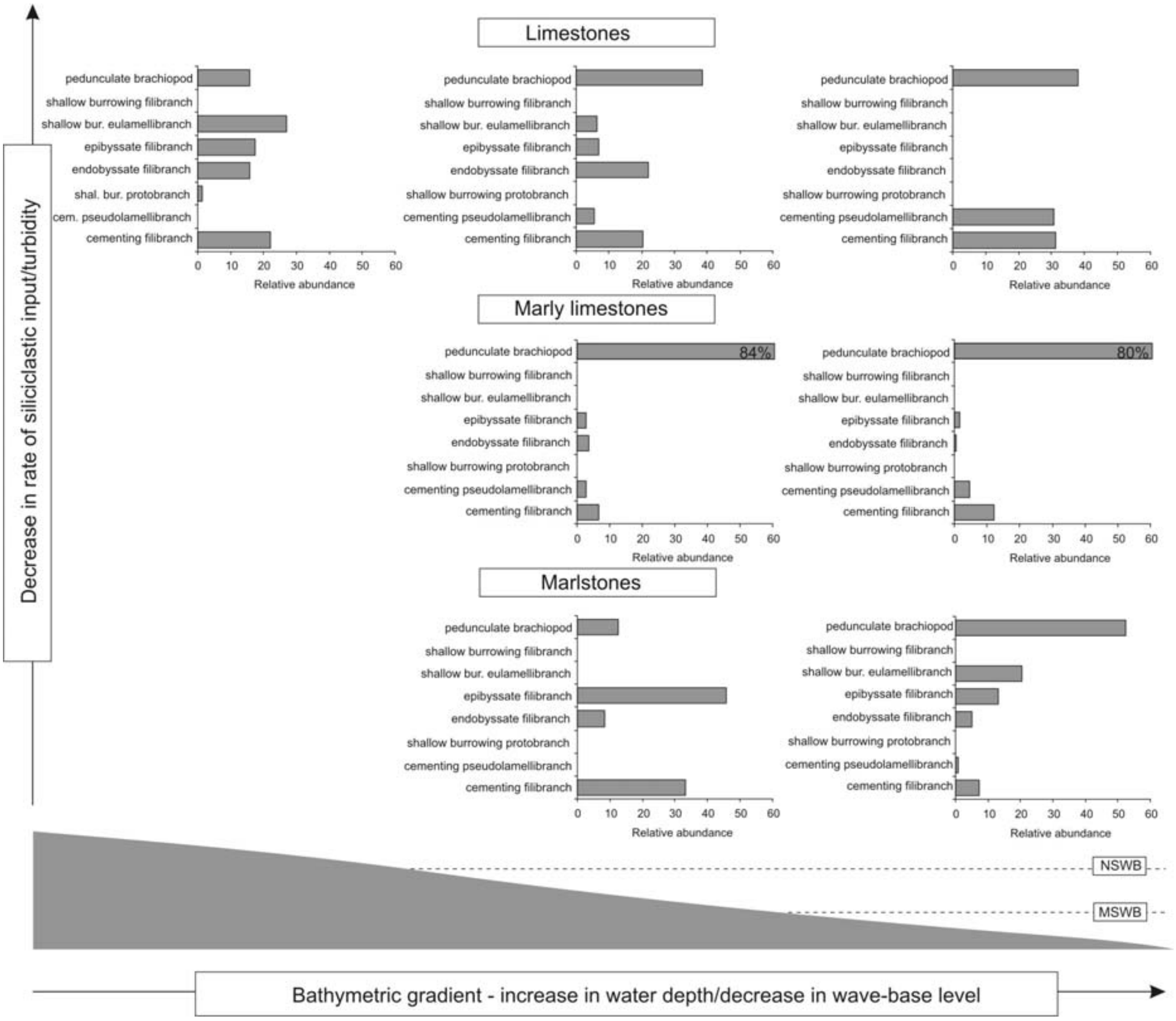


Figure 14 - Distribution of brachiopod and bivalve guilds along a gradient with varying siliciclastic supply and varying wave-base level.

Effects of wave-base level

One-way analyses. The compositional differences in sample-level relative abundances among habitats differing in the wave-base level (i.e., above FWWB, above NSWB, below NSWB and below MSWB) are rather low but significant both for species (R = 0.26, p = 0.0003) and guilds (R = 0.21, 0.0004). The differences in species abundances between habitats above FWWB and above NSWB, and between habitats below NSWB and below NSWB are very low and insignificant (Tab. 4). Other between-habitat pairwise comparisons based on species abundances are high and significant. The similar pattern follows from between-habitat pairwise comparisons based on guild abundances, although some significant differences become of borderline significance (Tab. 4). Habitats above

FWWB were dominated by cementing and epibyssate filibranchs (the *Placunopsis alpina* sample group; Fig. 14). Several guilds were abundant in the habitats above NSWB (Fig. 14), including pedunculate brachiopods (*Rhaetina gregaria*), cementing filibranchs (*Placunopsis alpina*), epibyssate filibranchs (*Rhaetavicula contorta*), endobyssate filibranchs (*Bakevellia praecursor*) and shallow burrowing eulamellibranchs (*Isocyprina ewaldi*). Habitats below NSWB and MSWB were dominated by pedunculate brachiopod *Rhaetina gregaria*, followed by less common cementing and endobyssate filibranchs, cementing pseudolamellibranchs and shallow burrowing eulamellibranchs (Fig. 14). The *G. inflata* sample group was limited to habitats below NSWB, the *R. gregaria-Actinostreon* sample groups to habitats below NSWB and MSWB, and the *R. gregaria-Zugmayerella* sample group to habitats below MSWB. Abundance of brachiopods and cementing psedolamellibranchs increased and abundance of cementing filibranchs and epibyssate bivalves decreased towards the deeper habitats. Shallow burrowing eulamellibranchs were most common in habitats above NSWB (Fig. 14).

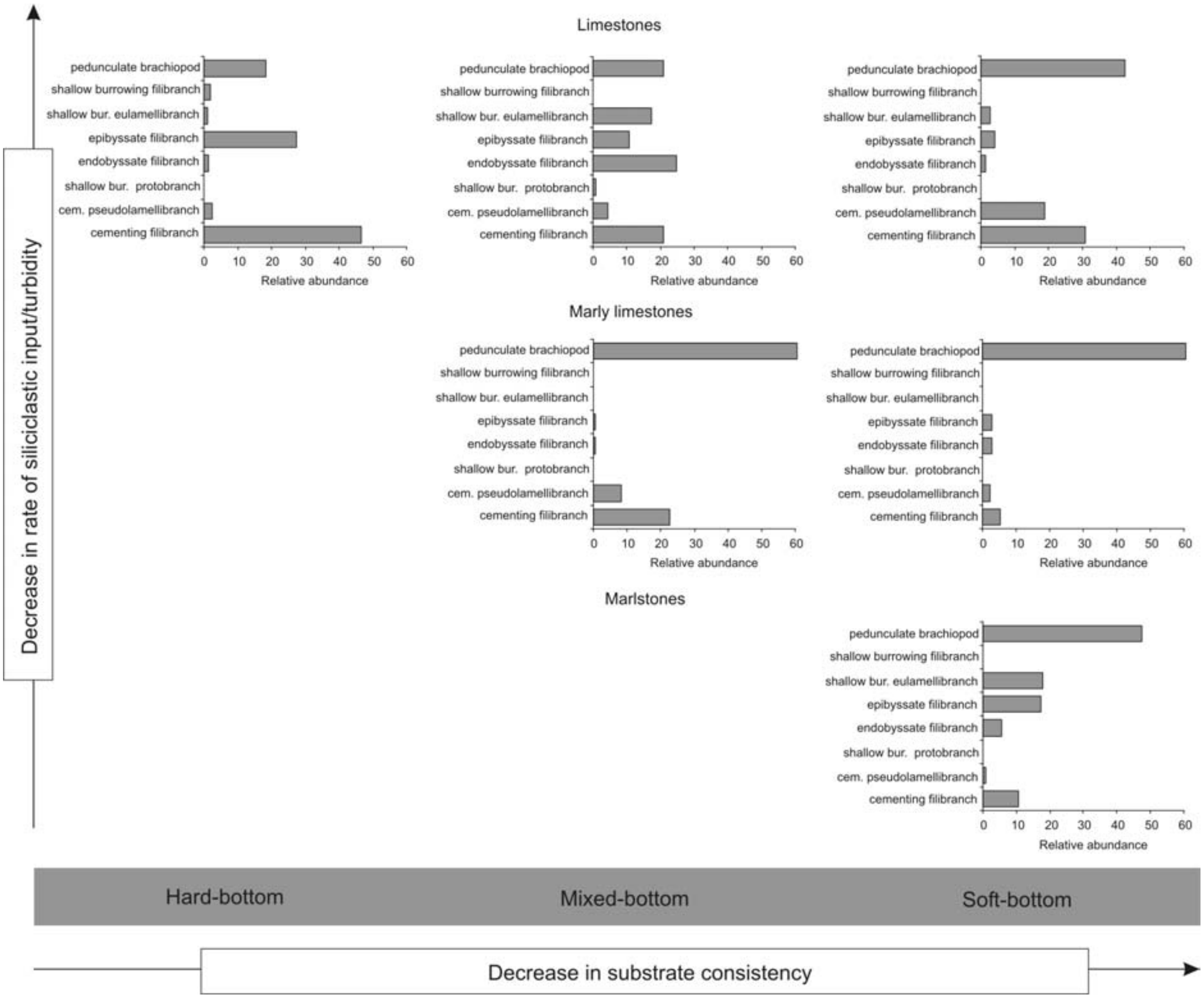


Figure 15 - Distribution of brachiopod and bivalve guilds with respet to varying siliciclastic supply and varying substrate consistency.

Separation of effects of siliciclastic supply. Two-way crossed ANOSIM tests whether there are any differences among habitats differing in the wave-base level, allowing for differences in siliciclastic supply. Keeping siliciclastic supply constant, there are no significant differences in species (R = 0.065, p = 0.13) and guild composition (R = 0.02, p = 0.32) among habitats differing in the wave-base level. When two-way crossed ANOSIM is separately performed for soft-bottom and mixed-bottom habitats, there are also no significant differences among habitats differing in the wave-base level for species composition (R [soft-bottom] = 0.013, p = 0.38, R [mixed-bottom] = 0.18, p = 0.11) and guild composition (R [soft-bottom] = 0.036, p = 0.31, R [mixed-bottom] = 0.14, p = 0.18).

One-way ANOSIM	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Species - habitats				
Global test	0.256	0.0003	10000	3
Below MSWB, Below NSWB	0.029	0.119	10000	1188
Below MSWB, Above FWWB	0.53	0.002	10000	22
Below MSWB, Above NSWB	0.485	0.003	10000	33
Below NSWB, Above FWWB	0.409	0.008	10000	79
Below NSWB, Above NSWB	0.404	0.008	10000	78
Above FWWB, Above NSWB	0.225	0.069	462	32
Guilds - habitats				
Global test	0.212	0.0004	10000	4
Below MSWB, Below NSWB	-0.007	0.502	10000	5021
Below MSWB, Above FWWB	0.421	0.006	10000	56
Below MSWB, Above NSWB	0.429	0.004	10000	35
Below NSWB, Above FWWB	0.39	0.0088	10000	88
Below NSWB, Above NSWB	0.346	0.012	10000	118
Above FWWB, Above NSWB	0.192	0.054	462	25

Two-way ANOSIM (habitat effects, allowing for siliciclastic effects)	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Species - habitats				
Global test	0.065	0.131	10000	1309
Guilds - habitats				
Global test	0.022	0.315	10000	3154

Two-way ANOSIM (habitat effects, allowing for substrate effects)	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Species - habitats				
Global test	0.108	0.105	10000	1052
Guilds - habitats				
Global test	0.09	0.135	10000	1351

Table 6 - Analysis of similarities (ANOSIM) showing differences in species abundance and guild abundances among habitats differing in the wave-base level. Effects of wave-base level are tested with (1) one-way analyses that do not take into account effects of other factors, (2) two-way crossed analyses that keep siliciclastic supply constant, and (3) two-way crossed analyses that keep substrate consistency constant. The p-value in bold indicate the differences that are significant. Applying the Bonferroni correction lowers the alpha value for pairwise comparisons to 0.0083 (0.05/6).

Separation of substrate effects. Two-way crossed ANOSIM tests whether there are any differences among habitats differing in the wave-base level, allowing for differences in substrate consistency. Keeping substrate properties constant, there are no significant differences in species (R = 0.11, p = 0.11) and guild composition (R = 0.09, p = 0.14) among habitats differing in the wave-base level. Because substrate types co-vary with differences in siliciclastic supply, the differences among habitats differing in the wave-base level were further separately evaluated for marly limestones and limestones. In marly limestones, two-way crossed ANOSIM shows that there are no significant differences in species (R = 0.034, p = 0.3) and guild composition (R = 0.12, p = 0.11) among habitats differing in the wave-base level. In contrast, in limestones, two-way crossed ANOSIM shows that there are significant differences in species (R = 0.44, p = 0.0079) and guild composition (R = 0.32, p = 0.044) among habitats differing in the wave-base level.

Effects of substrate consistency

One-way analyses. Differential effects of substrate consistency on community composition are demonstrated by significant differences among soft-bottom, mixed-bottom and hard-bottom habitats both for the species (R = 0.29, p = 0.0007) and guilds (R = 0.265, p = 0.0009). Pairwise comparisons indicate that the differences are significant between soft and mixed substrates, and between soft and hard substrates both for the species and guild abundances (Tab. 4). Surprisingly, relative abundance of pedunculate brachiopods increased towards deposits with lower substrate consistency (Fig. 15). In contrast, relative abundance of cementing and epibyssate filibranchs increased towards hard substrates with higher substrate firmness. Endobyssate filibranchs and shallow burrowing eulamellibranchs were abundant mainly in mixed-bottom habitats (Fig. 15).

Separation of effects of siliciclastic supply. Two-way crossed ANOSIM tests whether there are any differences among habitats differing in the substrate consistency, allowing for differences in siliciclastic supply. Keeping siliciclastic supply constant, soft-bottom habitats differ in community composition from mixed-bottom (R[species] = 0.37, p = 0.0087; R [guilds] = 0.26, p = 0.036) and hard-bottom habitats (R[species] = 0.39, p = 0.037; R [guilds] = 0.24, p = 0.065). When two-way crossed ANOSIM is separately performed for habitats differing in the wave-base level, there are also no significant differences among habitats differing in the substrate consistency for species composition (R[below NSWB] = 0.17, p = 0.14) and guild composition (R[below NSWB] = 0.057, p = 0.32).

Separation of wave-base level effects. Two-way crossed ANOSIM tests whether there are any differences among habitats differing in the substrate consistency, allowing for differences with respect to wave-base level. When wave-base level is kept constant, the differences among habitats differing in the substrate consistency are insignificant for species (R = 0.17, p = 0.17) and guild composition (R = 0.17, p = 0.18). When two-way crossed ANOSIM is separately performed for habitats differing in the intensity of siliciclastic supply, the results based on limestones differ from those based on marly limestones. In limestones, two-way crossed ANOSIM shows that the differences among habitats differing in the substrate consistency are insignificant for species (R = 0.02, p = 0.44) and guild composition (R = 0.09, p = 0.31). In contrast, in marly limestones, the differences among habitats differing in the substrate consistency are relatively high and significant for species (R = 0.66, p = 0.0004) and guild composition (R = 0.49, p = 0.026).

Comparison between level-bottom and patch-reef habitats

Differences in community composition are also evaluated for level-bottom and patch-reef habitats with coral colonies/coral debris. To exclude effects of other factors and decrease compositional variation, this comparison is restricted to the *Rhaetina gregaria* sample group. Six samples contain corals and 13 samples reflect level-bottom conditions. Surprisingly, the differences in the species (R = 0.047, p = 0.316) and guild abundances (R = 0.171, p = 0.1) between level-bottom and coral patch-reef habitats are very low and insignificant. In addition to *Rhaetina gregaria* (84.9%), the samples with corals contain abundant *Atreta intusstriata* (13%). Abundance of other species is below 1%. In contrast, *Rhaetina gregaria* is associated with several brachiopods *(Z. uncinata, A.*

cornigera) and bivalves (*G. inflata, A. haindigerianum, Atreta intusstriata, Pteria* sp. A) in level-bottom habitats. In addition, coral habitats have significantly lower median alpha species richness (2.7 species for n = 50) than level-bottom habitats (4.8 species for n = 50, Wilcoxon rank sum test, p = 0.0019). The differences between coral and level-bottom habitats in the evenness are insignificant (Wilcoxon rank sum test, p = 0.31 for PIE, p = 0.83 for J).

One-way ANOSIM	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Species - substrate				
Global test	0.29	0.0007	10000	7
floatstone, floatstone/packstone	0.274	0.004	10000	42
floatstone, packstone/rudstone	0.435	0.005	10000	50
floatstone/packstone, packstone/rudstone	-0.111	0.914	10000	9135
Guilds - substrate				
Global test	0.265	0.0009	10000	9
floatstone, floatstone/packstone	0.244	0.006	10000	57
floatstone, packstone/rudstone	0.402	0.006	10000	64
floatstone/packstone, packstone/rudstone	-0.061	0.696	10000	6964

Two-way ANOSIM substrate effects, allowing for siliciclastic effects)	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Species - substrate				
Global test	0.293	0.011	10000	108
floatstone, floatstone/packstone	0.367	0.0087	10000	87
floatstone, packstone/rudstone	0.388	0.037	462	17
floatstone/packstone, packstone/rudstone	-0.076	0.75	8008	6047
Guilds - substrate				
Global test	0.212	0.036	10000	358
floatstone, floatstone/packstone	0.258	0.038	10000	376
floatstone, packstone/rudstone	0.237	0.065	462	30
floatstone/packstone, packstone/rudstone	0.016	0.35	8008	2784

Two-way ANOSIM (substrate effects, allowing for habitat effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - substrate				
Global test	0.168	0.166	10000	1663
Guilds - substrate				
Global test	0.167	0.181	10000	1805

Table 7 - Analysis of similarities (ANOSIM) showing differences in species abundance and guild abundances among habitats differing in the substrate consistency. Effects of siliciclastic supply are tested with (1) one-way analyses that do not take into account effects of other factors, (2) two-way crossed analyses that keep siliciclastic supply constant, and (3) two-way crossed analyses that keep wave-base level constant. The p-value in bold indicate the differences that are significant. Applying the Bonferroni correction lowers the alpha value for pairwise comparisons to 0.017 (0.05/3).

Discussion

Richness and evenness. The higher species richness and evenness in bivalve- than in brachiopod-dominated samples may indicate inherently different community structure in bivalve-dominated communities. The between-community variations in species richness and evenness are coupled with habitat differences because the samples from shallower habitats show higher species richness and evenness than the samples from deeper habitats. Shallower, high-energy habitats may be characterized by higher habitat heterogeneity than deeper level-bottom habitats. Some differences in diversity can be of taphonomic nature because rudstones with the highest species richness show signs of long-term storm-reworking, possibly leading to between-habitat mixing. They can be also affected by high degree of time-averaging because of lower net sedimentation rate in habitats with frequent sediment winnowing and erosion. The differences in the alpha richness between brachiopod and bivalve samples become insignificant when the variation due to habitat differences is removed. It seems that differences in the alpha diversity between brachiopod and bivalve communities in the Fatric Basin were mainly driven by environmental differences.

When diversity patterns of brachiopod-dominated samples were evaluated separately, benthic communities in habitats with corals, probably associated with spatially heterogeneous conditions, had lower species richness than benthic communities from level-bottom habitats. Although this pattern is probably counter-acted by higher diversity of corals and sponges, the lower number of brachiopod and bivalve species in coral habitats might be caused by taphonomic and/or ecologic factors. First, very low species richness and evenness of the communities of coral patch-reefs may be enhanced owing to patchy distribution *Rhaetina gregaria*. The species richness and evenness can be depressed because it is possible that the sample coverage on the scale of several decimeters did not exceed the size of the patch. Second, the samples from coral patch-reefs are invariably represented by lithified limestones, in contrast to less lithified marly limestones or marlstones that represent level-bottom habitats. This difference can enhance diversity of level-bottom habitats because of higher sampling efficiency in poorly lithified samples. With respect to local ecological processes, the lower number of brachiopod and bivalve species in coral patch-reefs might be caused by competitive exclusion in habitats with dense framework of corals, sponges, algae and encrusters.

Habitat preferences of brachiopods and bivalves. In terms of Bray-Curtis similarities, the higher co-occurrence of brachiopods with mostly epifaunal, filibranch and pseudolamellibranch bivalves than with infaunal eulamellibranch bivalves is in accord with differential habitat preferences brachiopods and bivalves observed in other studies. Brachiopods thus shared higher similarity in habitat preferences to filibranch and pseudolamellibranch bivalves than to eulamellibranch bivalves. Differential habitat preferences between brachiopods and eulamellibranch bivalves are also supported by the significantly positive R value based on R-mode ANOSIM. In addition, substantial differences in habitat preferences between brachiopods and filibranchs are also indicated by their significantly different abundance patterns.

Differences in environmental distribution among epifaunal bivalves, infaunal bivalves, and brachiopods in the Fatric intra-shelf basin also indicate that niche preferences of their constituent species were consistently different. Their environmental distribution correlated to some degree with differences in siliciclastic supply, wave-base level and substrate consistency. In general, brachiopods were more common in deeper, mixed-bottom habitats with marly sediments. Epifaunal bivalves increased in abundance towards shallower, carbonate-rich habitats with coarse-grained sediments. Infaunal bivalves increased in abundance with increasing siliciclastic supply, and were mainly common at intermediate depths in mixed- and soft-bottom habitats. However, because variations in siliciclastic supply, wave-base level and substrate consistency co-varied to some degree, these general differences in environmental preferences are partly affected by interactions between these three factors. Variations in siliciclastic and carbonate supply showed significant effects on species and guild composition even when wave-base level and substrate consistency were kept constant. Variations in wave-base level showed significant effects on community composition mainly in interaction with varying siliciclastic supply and substrate consistency. For example, habitats above FWWB were characterized by relatively unique community composition, but such habitats were also invariably characterized by carbonate-rich and hard-bottom conditions. When substrate consistency was kept constant in carbonate-rich habitats (i.e., limestones), the differences among habitats with constant substrate consistency but differing in the wave base level had significant effects on community composition. However, variations in wave-base level had no significant effects on community composition of marly limestones. Variations in substrate consistency showed significant effects on community composition mainly in interaction with varying siliciclastic supply and wave-base level. When wave-base level was kept constant, variations in substrate consistency had significant effects on community composition of marly limestones. However, when wave-base level was kept constant, variations in substrate consistency did not show any significant effects on community composition of limestones.

Temporal within-sequence replacements indicate that environmental segregation of brachiopod and bivalve communities was probably primarily driven by varying levels of turbidity and nutrient supply that were substantially reduced during rapid shoreline retrogradation. The increase in abundance of brachiopods might be related to decreasing levels of turbidity and nutrient supply because the shoreline retrogradation was associated with the decrease in siliciclastic supply and with the onset of coral thickets and small-scale patch-reefs. This explanation is consistent with the hypothesis that brachiopods prefer habitats that are in more distal position with respect to siliciclastic and land-derived nutrient input than bivalves. In addition, in terms of biotic transitions, this relatively rapid replacement is more in accord with the scenario of physical perturbation that removes incumbents rather with the scenario of local biotic interactions that gradually sum into biotic replacement.

Conclusions

Brachiopods and bivalves that inhabited the intra-shelf Fatric Basin in the Late Triassic significantly differed in abundance patterns. In term of Bray-Curtis similarities, pedunculate brachiopods co-occurred more commonly with epifaunal, filibranch and pseudolamellibranch bivalves than with infaunal eulamellibranch bivalves. Brachiopods increased in abundance towards deeper habitats and were mainly abundant in mixed-bottom habitats with marly sediments. Epifaunal bivalves increased in abundance towards shallower, carbonate-rich and hard-bottom habitats. Infaunal bivalves increased in abundance with increasing siliciclastic supply, and were mainly common at intermediate depths in mixed- and soft-bottom habitats. Onshore-offshore distribution patterns of brachiopods and bivalves substantially changed within depositional sequences between intervals characterized by shoreline retrogradation and progradation. Brachiopods dominated both in shallow and deep habitats during shoreline retrogradation and onset of coral communities owing to relatively rapid sea level rise. In contrast, bivalves dominated in shallow and deep habitats mainly during shoreline progradation. Within-sequence replacement thus implies that varying nutrient and siliciclastic supply might primarily govern environmental segregation of brachiopods and bivalves. Differences in distribution patterns between brachiopods and epifaunal and infaunal bivalves are comparable to those observed in the Kössen Basin and can be explained by hypotheses that follows from actualistic observations. The dominance of brachiopods in mixed- and soft-bottom habitats can be explained by varying levels of turbidity and land-derived nutrient supply that were reduced during rapid shoreline retrogradation.

Reduced food supply might account for low abundance of infaunal bivalves and thus reduced sediment disturbance in soft-bottom habitats under transgressive conditions.

	B9.4	B9.5	B12	B9.4.2	B9.4.3	B9.5.1	B9.5.2	B10	B15.2	B12.7	D4.2	T4	T5	T6	T6.2	T7.4	T10	T17	T17.2	K1.2
Discinisca suessi	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thecospira haidingeri	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella uncinata	30	4	55	33	11	0	2	0	1	1	0	0	17	4	3	9	0	2	0	0
Rhaetina gregaria	67	102	156	78	59	45	102	73	84	57	167	0	3	1	3	51	72	37	6	3
Rhaetina pyriformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Austrirhynchia cornigera	1	1	5	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Nuculana claviformis	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Parallelodon sp. A	0	0	0	0	0	0	1	2	0	0	0	2	7	2	4	0	0	0	0	0
Parallelodon sp. B	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Catella sp.	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus minutus	1	0	3	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0
Pteria sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	1	0	0	0
Rhaetavicula contorta	0	0	0	1	1	0	0	0	0	0	1	2	18	3	0	1	4	0	0	11
Gervillaria inflata	2	4	1	0	2	5	10	3	0	0	0	0	2	0	0	0	0	0	0	0
Gervillia caudata	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Bakevellia praecursor	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0
Pinna sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Propeamussium schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Chlamys valoniensis	0	0	0	0	1	0	0	0	0	0	0	2	11	3	3	0	5	0	0	0
Chlamys sp. A	1	1	0	1	1	0	1	0	1	0	0	5	13	0	3	0	3	0	0	0
Atreta intusstriata	5	2	11	3	8	0	2	0	3	1	1	7	4	2	9	1	1	17	10	8
Placunopsis alpina	0	1	0	0	0	0	2	0	0	0	0	8	82	56	14	0	3	0	0	0
Antiquilima aff. *alpis*	0	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0
Antiquilima sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. A	0	0	0	0	0	0	0	0	0	0	0	2	5	2	0	0	0	0	0	0
Plagiostoma punctatum	1	2	1	2	0	1	1	0	3	0	0	0	0	0	0	0	1	0	0	0
Ostreid sp.	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Liostrea sp.	0	0	3	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Actinostreon haidingerianum	0	4	2	1	6	1	0	1	0	0	0	1	0	0	2	0	0	0	6	0
Gruenewaldia inflata	0	0	0	0	0	0	0	1	0	0	0	2	0	3	1	0	0	0	0	0
Elegantinia emmrichi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myophoriopis isoceles	0	2	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0
Pseudocorbula ewaldi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeocardita sp.	0	0	0	0	0	0	2	15	0	0	0	0	3	1	0	0	0	0	0	0
Protocardia rhaetica	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isocyprina alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myoconcha sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cornucardia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Costatoria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 - Absolute abundances of brachiopods and bivalves.

	K5	K31a	K31.2	K31.3	K31.4	K60	K2-51	K2-1	K2-2	D2.2	D26.3	BO4.4	S77	S77.2-1	S77.2-2	S78	S81.1	R35	RM	VF320
Discinisca suessi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thecospira haidingeri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zugmayerella uncinata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Rhaetina gregaria	0	234	161	94	12	87	0	0	0	0	0	0	0	0	0	0	191	16	0	186
Rhaetina pyriformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	36	0	0
Austrirhynchia cornigera	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32
Nuculana claviformis	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Parallelodon sp. A	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parallelodon sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Catella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus minutus	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	21	1	4	0
Pteria sp. A	0	0	0	0	0	3	0	0	0	0	7	0	0	0	0	0	18	0	0	0
Rhaetavicula contorta	0	0	0	0	0	0	9	6	5	7	37	0	1	9	14	1	0	0	0	0
Gervillaria inflata	61	0	0	0	0	0	8	0	1	0	0	0	0	0	0	0	0	0	8	0
Gervillia caudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bakevellia praecursor	0	0	0	0	0	0	0	0	0	2	0	25	1	5	6	0	0	0	0	0
Pinna sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Propeamussium schafhaeutli	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys valoniensis	0	0	0	0	0	0	1	0	0	32	4	0	0	0	0	0	0	0	0	0
Chlamys sp. A	0	0	1	1	1	0	1	0	1	1	0	0	1	0	0	2	0	1	0	0
Atreta intusstriata	0	45	29	3	6	1	1	0	1	3	0	0	2	0	0	1	14	1	0	0
Placunopsis alpina	1	0	0	0	0	0	5	1	4	126	82	29	6	1	2	8	0	0	1	1
Antiquilima aff. *alpis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0
Antiquilima sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Plagiostoma sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma punctatum	0	0	3	0	1	1	0	0	0	1	0	0	0	0	0	0	4	0	0	0
Ostreid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liostrea sp.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon haidingerianum	0	0	0	0	13	1	0	0	0	0	0	0	0	0	0	0	0	1	0	3
Gruenewaldia inflata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elegantinia emmrichi	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myophoriopis isoceles	1	0	0	0	0	0	1	16	6	0	0	0	1	1	2	0	0	0	0	0
Pseudocorbula ewaldi	0	0	0	0	0	0	0	2	0	0	0	0	3	4	5	1	0	0	0	0
Palaeocardita sp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0
Protocardia rhaetica	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
Isocyprina alpina	25	0	0	0	0	0	0	0	0	0	0	0	2	17	10	1	0	0	0	0
Myoconcha sp.	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornucardia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardium sp.	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0
Costatoria sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) – Absolute abundances of brachiopods and bivalves.

	VF1	VF2	ZV8	ZV15	ZV16	ZV17	BOS
Discinisca suessi	0	0	0	0	0	0	0
Thecospira haidingeri	0	0	0	0	0	0	0
Zugmayerella uncinata	0	38	0	0	1	1	0
Rhaetina gregaria	59	62	99	7	12	12	127
Rhaetina pyriformis	0	0	0	0	0	0	0
Austrirhynchia cornigera	5	0	0	0	0	0	0
Nuculana claviformis	0	0	0	0	0	0	0
Parallelodon sp. A	0	0	0	0	0	0	0
Parallelodon sp. B	0	0	0	0	0	0	0
Catella sp.	0	0	0	0	0	0	0
Modiolus minutus	0	0	0	0	0	0	0
Pteria sp. A	0	0	0	0	0	0	0
Rhaetavicula contorta	0	0	0	0	0	0	0
Gervillaria inflata	0	0	0	0	0	0	0
Gervillia caudata	0	0	0	0	0	0	0
Bakevellia praecursor	0	0	0	0	0	0	0
Pinna sp. A	0	0	0	0	0	0	0
Propeamussium schafhaeutli	0	0	0	0	0	0	0
Chlamys valoniensis	0	0	0	0	0	0	1
Chlamys sp. A	1	2	0	0	0	0	0
Atreta intusstriata	5	2	16	3	11	14	5
Placunopsis alpina	0	0	0	0	0	1	0
Antiquilima aff. *alpis*	0	0	0	0	0	0	0
Antiquilima sp. A	0	0	0	0	0	0	0
Plagiostoma sp. A	0	0	0	0	0	0	0
Plagiostoma punctatum	0	0	0	0	0	0	1
Ostreid sp.	0	0	0	0	0	0	0
Liostrea sp.	0	0	0	0	0	0	0
Actinostreon haidingerianum	10	6	5	11	6	7	0
Gruenewaldia inflata	0	0	0	0	0	0	0
Elegantinia emmrichi	0	0	0	0	0	0	0
Myophoriopis isoceles	0	0	0	0	0	0	0
Pseudocorbula ewaldi	0	0	0	0	0	0	0
Palaeocardita sp.	0	0	0	0	0	0	0
Protocardia rhaetica	0	0	0	0	0	0	0
Isocyprina alpina	0	0	0	0	0	0	0
Myoconcha sp.	0	0	0	0	0	0	0
Cornucardia sp.	0	0	0	0	0	0	0
Cardium sp.	0	0	0	0	0	0	0
Costatoria sp.	0	0	0	0	0	0	0

Supplement 1 (cont.) – Absolute abundances of brachiopods and bivalves.

Species	Guild
Discinisca suessi	pedunculate brachiopod
Thecospira haidingeri	cementing brachiopod
Zugmayerella uncinata	pedunculate brachiopod
Rhaetina gregaria	pedunculate brachiopod
Rhaetina pyriformis	pedunculate brachiopod
Austrirhynchia cornigera	pedunculate brachiopod
Nuculana claviformis	deposit shallow burrower
Parallelodon sp. A	epibyssate filibranch
Parallelodon sp. B	epibyssate filibranch
Catella sp.	endobyssate filibranch
Modiolus minutus	endobyssate filibranch
Pteria sp. A	epibyssate filibranch
Rhaetavicula contorta	epibyssate filibranch
Gervillaria inflata	endobyssate filibranch
Gervillia caudata	epibyssate filibranch
Bakevellia praecursor	endobyssate filibranch
Pinna sp. A	endobyssate filibranch
Propeamussium schafhaeutli	free-lying filibranch
Chlamys valoniensis	epibyssate filibranch
Chlamys sp. A	epibyssate filibranch
Atreta intusstriata	cementing filibranch
Placunopsis alpina	cementing filibranch
Antiquilima aff. alpis	epibyssate filibranch
Antiquilima sp. A	epibyssate filibranch
Plagiostoma sp. A	epibyssate filibranch
Plagiostoma punctatum	epibyssate filibranch
Ostreid sp.	cementing pseudolemallibranch
Liostrea sp.	cementing pseudolemallibranch
Actinostreon haidingerianum	cementing pseudolemallibranch
Gruenewaldia inflata	shallow burrowing filibranch
Elegantinia emmrichi	shallow burrowing filibranch
Myophoriopis isoceles	eulamellibranch shallow burrower
Pseudocorbula ewaldi	eulamellibranch shallow burrower
Palaeocardita sp.	eulamellibranch shallow burrower
Protocardia rhaetica	eulamellibranch shallow burrower
Isocyprina alpina	eulamellibranch shallow burrower
Myoconcha sp.	endobyssate filibranch
Cornucardia sp.	epibyssate filibranch
Cardium sp.	eulamellibranch shallow burrower
Costatoria sp.	shallow burrowing filibranch

Supplement 2 – Guild assignments of brachiopods and bivalves

Sample	Sample group	Facies	Sediment	Habitat	Sequence
T4	*P. alpina*	packstone/rudstone	Limestone	Above FWWB	1
T5	*P. alpina*	packstone/rudstone	Limestone	Above FWWB	1
T6	*P. alpina*	packstone/rudstone	Limestone	Above FWWB	1
T6.2	*P. alpina*	packstone/rudstone	Limestone	Above FWWB	1
D26.3	*P. alpina*	packstone/rudstone	Limestone	Above FWWB	4
T10	*R. gregaria*	packstone/rudstone	Limestone	Above NSWB	1
K1.2	*R. contorta*	floatstone	Marlstone	Above NSWB	1
BO4.4	*P. alpina*	floatstone/packstone	Limestone	Above NSWB	1
S77	*P. alpina*	floatstone/packstone	Limestone	Above NSWB	1
S77.2-1	*R. contorta*	floatstone/packstone	Limestone	Above NSWB	1
S77.2-2	*R. contorta*	floatstone/packstone	Limestone	Above NSWB	1
B9.4	*R. gregaria - Z. uncinata*	floatstone	Marlstone	Below MSWB	3
B12	*R. gregaria - Z. uncinata*	floatstone	Marly limestone	Below MSWB	3
B9.4.2	*R. gregaria - Z. uncinata*	floatstone	Marlstone	Below MSWB	3
B9.4.3	*R. gregaria - Z. uncinata*	floatstone	Marly limestone	Below MSWB	3
B15.2	*R. gregaria*	floatstone	Marlstone	Below MSWB	3
T7.4	*R. gregaria*	floatstone	Marly limestone	Below MSWB	1
T17.2	*R. gregaria - A. haidingerianum*	floatstone/packstone	Marly limestone	Below MSWB	1
K31a	*R. gregaria*	floatstone	Marly limestone	Below MSWB	2
K31.2	*R. gregaria*	floatstone	Marly limestone	Below MSWB	2
K31.3	*R. gregaria*	floatstone	Marly limestone	Below MSWB	2
K2-51	*R. contorta*	floatstone	Marlstone	Below MSWB	4
K2-1	*R. contorta*	floatstone	Marlstone	Below MSWB	4
K2-2	*R. contorta*	floatstone	Marlstone	Below MSWB	4
VF2	*R. gregaria - Z. uncinata*	floatstone	Marlstone	Below MSWB	1
ZV15	*R. gregaria - A. haidingerianum*	floatstone	Limestone	Below MSWB	1
ZV16	*R. gregaria - A. haidingerianum*	floatstone	Limestone	Below MSWB	1
ZV17	*R. gregaria - A. haidingerianum*	floatstone	Limestone	Below MSWB	1
BOS	*R. gregaria*	floatstone	Marly limestone	Below MSWB	4
B9.5	*R. gregaria*	floatstone	Marly limestone	Below NSWB	3
B9.5.1	*R. gregaria*	floatstone	Marly limestone	Below NSWB	3
B9.5.2	*R. gregaria*	floatstone	Marly limestone	Below NSWB	3
B10	*R. gregaria*	floatstone/packstone	Limestone	Below NSWB	3
B12.7	*R. gregaria*	floatstone	Marly limestone	Below NSWB	3
D4.2	*R. gregaria*	floatstone/packstone	Limestone	Below NSWB	1
T17	*R. gregaria*	floatstone/packstone	Marly limestone	Below NSWB	1
K5	*G. inflata*	floatstone/packstone	Limestone	Below NSWB	1
K31.4	*R. gregaria - A. haidingerianum*	floatstone/packstone	Limestone	Below NSWB	2
K60	*R. gregaria*	floatstone	Marly limestone	Below NSWB	3
D2.2	*P. alpina*	floatstone/packstone	Limestone	Below NSWB	1
S78	*P. alpina*	floatstone	Limestone	Below NSWB	1
S81.1	*R. gregaria*	floatstone	Marly limestone	Below NSWB	1
R35	*R. pyriformis*	floatstone/packstone	Marly limestone	Below NSWB	3
RM	*G. inflata*	floatstone/packstone	Limestone	Below NSWB	1
VF320	*R. gregaria*	floatstone	Limestone	Below NSWB	1
VF1	*R. gregaria*	floatstone	Marly limestone	Below NSWB	1
ZV8	*R. gregaria*	floatstone/packstone	Marly limestone	Below NSWB	1

Supplement 3 - Environmental and stratigraphic assignments.

5. Ecology of brachiopods and bivalves in the Upper Triassic of the Hronic Unit (West Carpathians)

(with Marián Golej, Jozef Michalík, and Ján Schlögl)

Abstract. Upper Triassic communities dominated by brachiopods and epifaunal bivalves that inhabited an intra-platform basin of the West Carpathians (Hronic Unit) show significant differences between environments differing in the storm intensity, terrigenous supply and substrate type. Although some brachiopods were abundant in soft-bottom habitats below maximum storm wave base, they dominated mainly in shallow, carbonate-rich and mixed-bottom habitats above maximum storm wave base. Epifaunal bivalves dominated in marl-rich and soft-bottom habitats below maximum storm wave base. Bivalve communities show significantly higher alpha species richness and evenness than brachiopod communities but these differences are coupled with environmental differences. Analysis of similarities indicate that brachiopods co-existed more commonly with epifaunal, filibranch and pseudolamellibranch bivalves than with infaunal, eulamellibranch and protobranch bivalves. This differential co-existence implies differential habitat requirements of brachiopods, epifaunal bivalves and infaunal bivalves and is in accord with the actualistic observations about their distinct habitat requirements with respect to substrate, nutrient supply and turbidity levels. An increase in terrigenous supply and turbidity, possibly coupled with higher sediment-mediated biological disturbance due to higher abundance of infaunal bivalves, could be responsible for the decreased abundance of brachiopods in marl-rich habitats. An increased siliciclastic supply could also correlate with higher land-derived nutrient input that is beneficent for food supply requirements of infaunal bivalves. Replacements between communities dominated by brachiopods and bivalves in the Hybe Formation support the role of physical perturbations related to variations in siliciclastic supply in such biotic transitions.

Introduction

Long-term changes and transitions in environmental distribution, abundance and diversity of benthic marine invertebrates and their biotic interactions drive present-day paleoecologic analyses (Patzkowsky and Holland, 1993; Jacobs and Lindberg, 1998; Sepkoski et al., 2000; Novack-Gottshall and Miller, 2003a, b; Alroy, 2004; Peters, 2004; Finnegan and Droser, 2005; Kosnik, 2005; Kowalewski et al., 2005). One of these transitions includes a replacement of the Paleozoic evolutionary fauna with high turnover rates by the Modern evolutionary fauna with low turnover rates (Sepkoski, 1981, 1984). A replacement of brachiopod-dominated communities with low metabolic demands by bivalve-dominated communities with high metabolic demands in terms of their diversity and abundance during the Mesozoic is related to this class of biotic transitions. This replacement, either real or apparent, is variously interpreted as due to (1) preservation and sampling artifacts caused by higher preservation potential of brachiopods, (2) a bottleneck effect of the end-Permian mass extinction (Gould and Calloway, 1980), (3) increased escalation via higher predation and competition rates (Vermeij, 1977; Sepkoski, 1986), (4) increased bioturbation rates (Thayer, 1983) and/or (5) increased supply of energy and nutrients during the Phanerozoic (Bambach, 1993). Miller (1998, 2000) summarized three possible views on the main biotic transitions during the Phanerozoic. As he suggested, long-term diversity changes could be linked to (1) biotic interactions over extended intervals of geologic time, (2) to short-term global perturbations that led to mass extinctions and caused removal of incumbents or (3) they might be related to a sum of relatively rapid, physically-mediated local or regional perturbations (with mass extinctions forming the largest end-member along a continuum of physical perturbations). The second and third views assume that the replacement groups become dominant not owing to long-term biotic interactions but because incumbents are lost due to environmental disturbance (Miller, 2000). The biotic transitions should be in accord with the increased or decreased availability of particular habitats after physical perturbations. For example, if the physical perturbations cause that the proportion of terrigenous-rich habitats is increasing, the biota associated with terrigenous-rich habitats before the perturbation should increase in its abundance after the perturbation. This prediction enables to explicitly use analyses of local and regional faunal datasets for solving problems that are mostly phrased for global datasets (Patzkowsky and Holland, 1993).

The increase in sediment-mediated biological disturbance (Thayer, 1983) and/or the increase in predation intensity during the Mesozoic (Vermeij, 1977, 1994), which belong to one class of explanations for the replacement of brachiopod by bivalve communities, might be significant already in Late Triassic. Thayer (1983) published a set of Phanerozoic curves that show that a number of taxa with high reworking rates, number of deep burrowing taxa and maximum mean reworking depth substantially increased during the Triassic, usually followed by further increase in the Jurassic. Also, there is a large diversification of burrowing predators and deposit-feeders in the Triassic (Thayer, 1983), and some evidence that the increase in predation intensity could already started in the Late Triassic (Hautmann, 2004b; Nützel and Erwin, 2004). Analyses of local or regional co-existence patterns of Triassic brachiopod and bivalve communities and their spatial and temporal transitions can thus address questions related to the evolutionary ecology of brachiopods and bivalves.

Investigating the role of environmental factors that determine distribution of brachiopods and bivalves and their habitat requirements is the goal of this chapter. The aim is to describe brachiopod and bivalve communities in a Late Triassic marine, intra-platform embayment with the deposition of the Hybe Formation (Hronic Unit, West Carpathians), to explore relationship between brachiopod- and bivalve–dominated samples and among brachiopod and bivalve guilds, and to test for environmental effects that can correlate with community differences based on their diversity and taxonomic and guild composition.

Setting

The Hybe Formation (Rhaetian) consists of mixed, marl-carbonate deposits and belongs to the Hronic Unit, which forms a structurally highermost nappe complex (Choč Nappe) in the Central West Carpathians. Deposits of Rhaetian age are rarely preserved in the Hronic Unit. They are mainly represented by the Norovica Formation, which consists of well-bedded, oncoidal, peloidal and oolitic limestones comparable to the lagoonal facies of the Dachstein Formation (Gaździcki and Michalík, 1980). The only place in the Hronic Unit where the Hybe Formation is preserved is represented by the sections situated southeast of the Hybe village, within a meander of the Biely Váh River in the northern part of the Nízke Tatry Mountains (Fig. 1).

During Late Triassic, the Central West Carpathians were situated within an extensive carbonate platform on the northwestern margin of the Tethys Ocean in the subtropical climatic belt. This platform was subdivided into several, approximately shore-parallel settings that are presently preserved in different paleotectonic units (Michalík, 1980). In the most proximal, northern part of the carbonate platform, continental-lacustrine deposits deposited in the Tatric Unit were replaced in seaward direction by an intra-shelf, carbonate-dominated basin (Fatric Basin), now represented by the Fatra Formation with highly variable, peritidal to shallow subtidal facies associations. The Fatra Formation is preserved in the Fatric and Veporic units. Further to the south, shallow carbonate lagoons and tidal flats are represented by the Norovica and Dachstein formations preserved in the Hronic and Silicic units. The Hybe Formation probably represents a relict of an intra-platform basin or small embayment of more limited extent than the Fatric Basin, with varying rate of terrigenous sedimentation and facies associations that are less variable when compared to facies associations of the Fatra Formation.

Figure 1 - Geographic position of the Hybe locality in the northern Slovakia.

Sections

Although the Hybe Formation is not exposed in its whole thickness, it can be about 20 to 50 meters thick (Michalík et al. 1988). It overlies a succession consisting of oncoidal, oolitic and stromatolitic limestones that are comparable to the Norovica or Dachstein formations. The lower part of the Hybe Formation is formed by a carbonate-rich interval consisting of crinoidal, bioclastic and oolitic limestones. This interval is capped by a thick limestone with colonies of branching corals (*Retiophyllia*). Its upper part is formed by alternation of bioclastic and crinoidal limestones, marly limestones and marls (Michalík 1973a). The conodont *Misikella posthernsteini* found in this upper part proves the Upper Rhaetian *Choristoceras marshi* Zone. Serpulids, bryozoans, brachiopods, bivalves, and cephalopods described by Goetel (1917), Prantl (1938), Michalík (1975, 1976, 1977b), Ziegler and Michalík (1980), Taylor and Michalík (1991), Rakús (1992) and Golej (2005) were found in the upper part of the Hybe Formation. Brachiopods and bivalves analyzed in this study were also sampled in the upper part, which is presently exposed in two sections (Fig. 2).

The Šimkovičova section described by Michalík (1973a) exposes a 17 meters thick succession, which consists of crinoidal-bioclastic packstones, biomicritic wackestones, marly floatstones and marls. Synsedimentary slumps are present both in the lower and upper parts of the section (Michalík 1973a). The lower slump complex is formed by well sorted and densely packed crinoidal packstones, with bioclastic-crinoidal packstone beds dominated by the pedunculate brachiopod *Zugmayerella* *koessenensis* in its lowermost and uppermost parts (Fig. 2, beds 8 and 9). These beds with *Zugmayerella* are probably stratigraphically equivalent. Crinoidal, bioclastic-rich packstones, floatstones and rarely grainstones/rudstones are present in the middle part of the section (beds 9-26). Large bioclasts are represented predominantly by bivalve (*Plagiostoma subvaloniense*), brachiopod (*Z. koessenensis*, Rhynchonellid sp. A), gastropod crinoid and coral fragments. They are commonly convex-up oriented, loosely or densely packed and moderately sorted. Some beds are graded (bed 13) and moderately bioturbated with patchy and irregular distribution of bioclasts. Shell infillings with sparry calcite indicate that this part of the section is not overturned. Higher, this carbonate-rich interval is replaced by alternation of marls and highly bioturbated micritic mudstones and wackestones (beds 27-31). Mudstones/wackestones are rich in loosely-packed, silt-sized crinoidal and bioclastic debris. They contain the pedunculate brachiopod *Zeilleria norica*, bivalves and rare nautiloids. This interval is replaced by several meters thick, poorly-exposed folded slump-complex of crinoidal packstones, terminated by bed 32. This bed is overlain by an about 1 m-thick interval formed by bioclastic-rich and locally coquinal marls with marly limestone lenses or limestone beds in the upper part of the section. This interval is moderately bioturbated and it contains abundant brachiopods (*Zeilleria norica, Rhaetina pyriformis*) and bivalves. The marl is abruptly replaced by well sorted and densely packed calcarenitic/calciruditic limestone bed with a sharp and irregular base. An alternation of 10-20 cm-thick bioclastic packstones characterizes the uppermost part of the Šimkovičova section.

The Kantorská section exposes an about eight meters thick succession of the Hybe Formation (Fig. 2). It starts with one meter thick marl with micrite concretions at its base. The lower part of the section consists of thick-bedded, well/moderately sorted crinoidal packstones with rare fragments of large bioclasts (beds 1-7). An 80 cm-thick crinoidal-bioclastic packstone (bed 8) with dispersed fragments of bivalves and brachiopods is overlain by a 70 cm-thick bedset formed by small-scale alternation of dark grey, shell-rich marls and concretionary, shell-rich limestones. In this study, this bedset was subdivided into three, 20-30 cm thick beds (8.2-8.4) that were analyzed separately. Moderately bioturbated marls and limestones contain loosely/densely packed, poorly sorted and randomly oriented brachiopods (*R. pyriformis*) and bivalves, locally in small, cm-scale clusters. Limestones show cm-scale internal stratification consisting of one or two cm-thick layers of densely packed and well/moderately sorted shell debris that alternate with micrite-rich floatstones with poorly sorted and well preserved bioclasts. Fragmented and disarticulated shell debris is distributed irregularly or in clumps. Articulated shells are mostly completely filled with micrite. This bedset is sharply overlain by a 30 cm thick, graded coquinal rudstone/packstone with an irregular base (bed 9). The upper part of the section is formed by alternation of bioclastic marls and marly wackestones with abundant bivalves (*Rhaetavicula contorta, Chlamys valoniensis*), less common brachiopods and rare nautiloids (beds 10-16). Marls and marly wackestones show signs of slight bioturbation and are characterized by high proportions of disarticulated and fragmented shell debris, commonly in concordant orientation.

Stratigraphic correlation of the two sections is limited owing to the poor exposure, synsedimentary and postsedimentary tectonic deformations and lack of index species. A preliminary approach is based on linking beds 8.2-8.4 in the Kantorská section with bed 32.2 in the Šimkovičova section. First, both beds are overlying a relatively thick interval with well-bedded crinoidal packstones. Second, both beds are sharply overlain by packstone or rudstone with similar sedimentologic features. Third, species composition of these two beds is very similar.

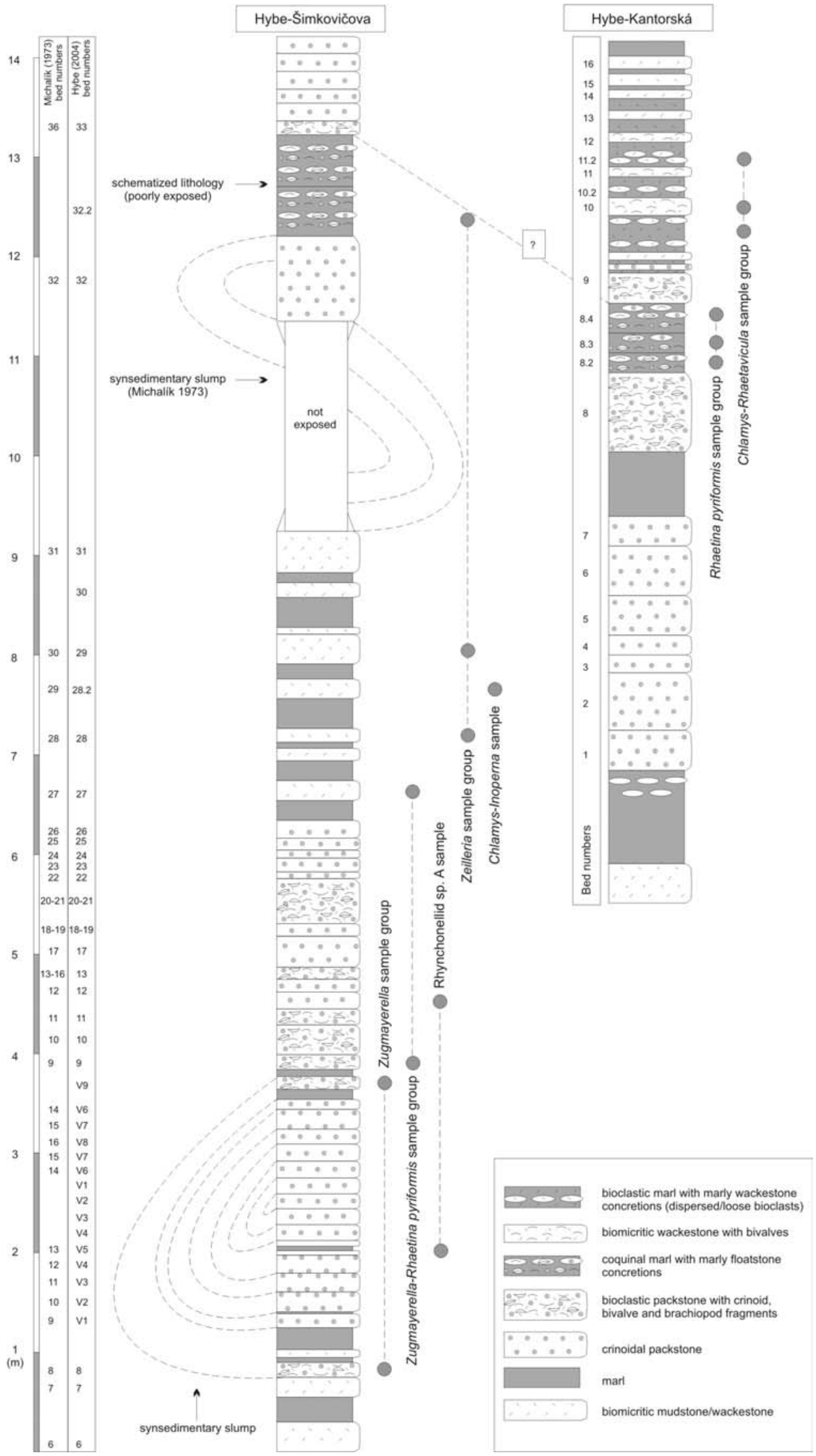


Figure 2 - Two stratigraphic sections (Hybe-Kantorská and Hybe-Šimkovičova), which show deposit types, synsedimentary slumps and vertical distribution of benthic communities in the upper part of the Hybe Formation.

Methods

A dataset based on field data consists of 17 samples and 1709 individuals. All the specimens collected within lithified or poorly lithified deposits with a lateral extent between 50-100 cm were counted. With the expections of the samples HK8a and HS32.2 that represent pooled averages of dm-scale marl/limestone couplets, all samples correspond to one bed. The absolute abundances of brachiopod and bivalve specimens were converted into number of individuals as the sum of articulated shells plus dominating number of either dorsal or ventral valves and standardized to relative abundances. The analyses were performed either on the species or guild level. Brachiopod and bivalve identifications were made using the papers of Michalík (1975, 1976, 1977b), Pearson (1977), Siblík (1998) and Golej (2005). Rhynchonellids determined as "*Rhynchonella"* ex gr. *subrimosa* by Siblík (1998) were assigned to Rhynchonellid sp. A.

Bivalves were classified into ten guilds according to their substrate relationship (Aberhan, 1994) and gill type (Stanley, 1968) and brachiopods into a cementing, pedunculate guild with a functional pedicle and free-lying guild (Alexander, 1977). Two brachiopod species were assigned to the free-lying brachiopod guild. *Oxycolpella oxycolpos* possesses very small pedicle opening, extreme secondary shell thickening in the posterior shell parts and its delthyrial cavity is substantially restricted via thick deltidial plate, pedicle collar and large cardinal process. Rhynchonellid sp. A has highly biconvex shells, secondary shell thickenings in the delthyrial and notothyrial cavities and incurved ventral beak with small pedicle opening. With the exception of the cementing brachiopods *Thecospira* and *Bactrynium*, all other brachiopods were assigned to the pedunculate guild, although some of them could probably be also free-lying in the adult stage (e.g., *Zeilleria*).

Exploratory multivariate analyses used in this study include cluster analysis, non-metric multidimensional scaling (NMDS) and detrended correspondence analysis (DCA). NMDS does not make any assumptions about species distribution and is useful for representing variations in species composition in low number of dimensions. In contrast to NMDS, DCA is based on an underlying unimodal model of species distribution and its axes are scaled in units of species standard deviations (De`ath, 1999). Both methods were used complementarily in this paper. The Bray-Curtis (BC) similarities based on untransformed relative abundances were used in the cluster and NMDS analyses. In Q-mode analyses, the BC similarity corresponding to 100 means that two compared samples have identical species or guild abundances. If it is 0, two samples have no species or guilds in common. In R-mode analyses, the BC similarity corresponding to 100 indicates that abundances of two compared species or guilds are the same in all samples. The BC similarity corresponding to 0 indicates that two compared species or guilds have no samples in common.

For confirmatory purposes, one-way analysis of similarities (ANOSIM) was used for testing if average rank BC dissimilarity within habitats (Q-mode) or guilds (R-mode), is significantly lower than average rank BC dissimilarity between habitats or guilds (Clarke and Green, 1988). If the null hypothesis (e.g., there are no differences in composition among habitats) is rejected in Q-mode analyses, environmental variations significantly correlate with variations in community composition. Test statistic (R) attains the values from -1 to 1. It is zero if the null hypothesis is true, so average of rank dissimilarities between and within habitats are the same. Large values close to one are indicative of complete compositional separation of habitats. In R-mode analyses, if the R value is significantly higher than zero, the compared guilds substantially differ in their sample-level relative abundances.

The analyses were performed with the PRIMER and PAST softwares (Clarke and Warwick, 2001; Hammer et al., 2001).

Three tests that compare habitats with (1) distinct storm intensity and frequency, (2) different amount of terrigenous supply, and (3) different sediment packing were performed. Well/moderately sorted and densely packed crinoidal-bioclastic packstones with signs of amalgamation were assigned to habitats above normal storm wave base (NSWB), implying frequent storm disturbance. Poorly sorted and loosely packed marls and marly floatstones with thin, non-amalgamated layers of densely-packed and moderately-sorted shell debris were assigned to habitats below NSWB, indicating rare storm disturbance. Mudstones, wackestones and bioclastic marls with missing signs of high-energy disturbance were assigned to habitats below maximum storm wave base (MSWB).

Discrimination of sample groups

Q-mode cluster analysis of 17 samples with 1709 individuals with the group-average linking method discriminated five sample groups and two samples with a unique composition at Bray-Curtis similarity corresponding to 45 (Fig. 3). Four groups are dominated by pedunculate brachiopods and one group by epibyssate bivalves (Figs. 4-5). Two samples are dominated by the free-lying brachiopod Rhynchonellid sp. A and by epibyssate and endobyssate bivalves. The sample groups are comparable to the associations of Fürsich (1977) and to the paleocommunity types of Bambach and Bennington (1996). The dataset analysed in this study is shown in Table 1.

(1) The *Rhaetina pyriformis* sample group is represented by four samples with 630 individuals. The sample-level richness (S) is between 16 and 24, the evenness (PIE) is between 0.77 and 0.84. The pedunculate brachiopods *Rhaetina pyriformis* (39.8%), *Fissirhynchia fissicostata* (9.3%), *R. hybensis* (7.4%), *Zeilleria norica* (6.5%) and *Zugmayerella koessenensis* (4.9%) dominate. Cementing (*Actinostreon haidingerianum*), free-lying (*Cassianella inaequiradiata*) and epibyssate bivalves (*Chlamys simkovicsi*, *Chlamys valoniensis*) are also abundant. Endobyssate and shallow burrowing bivalves are rare (below 1%). This group occurs in dark-grey, bioturbated, bioclastic marlstones and marly floatstones. They locally contain 1 cm-thick packstone layers with well sorted and densely packed bioclastic debris. Bioclasts are loosely/densely packed, poorly sorted and randomly oriented. This group is present in the middle part of the Kantorská section (beds 8.2-8.4).

(2) The *Zugmayerella-Rhaetina pyriformis* sample group is represented by two samples and 59 individuals. The sample-level richness (S) is between 10 and 12, the evenness (PIE) is between 0.81 and 0.88. The pedunculate brachiopods *Zugmayerella koessenensis* (29.9%), *Rhaetina pyriformis* (20.2%) and *Zeilleria norica* (12.4%) are dominant. Epibyssate bivalves (*Parallelodon hettangiensis, Plagiostoma punctatum, P. subvaloniense*) are common (15.8%). Free-lying brachiopods (5%) and the endobyssate bivalves *Modiolus hybbensis* and *Inoperna (Triasoperna) schafhaeutli* (7.1%) are less common. Shallow burrowing bivalves are absent. This sample group occurs in biomicritic wackestones and floatstones/packstones in the lower and middle part of the Šimkovičova section (beds 9 and 27).

(3) The *Zugmayerella* sample group is represented by two samples with 146 individuals. The sample-level richness (S) is between 14 and 17, the eveness (PIE) is between 0.79 and 0.89. The pedunculate brachiopods *Zugmayerella koessenensis* (31.1%) and *Zeilleria norica* (8.3%), the epibyssate bivalve *Plagiostoma subvaloniense* (15%), and the cementing bivalves *Atreta intusstriata* (10.9%) and *Actinostreon haidingerianum* (9.7%) are dominant. Endobyssate bivalves and free-lying

brachiopods are less common (below 5%) and shallow burrowing bivalves are rare (below 1%). This group occurs in well/moderately sorted and densely packed bioclastic packstones/floatstones with coral and crinoid debris in the lower part of the Šimkovičova section (beds 8 and V9).

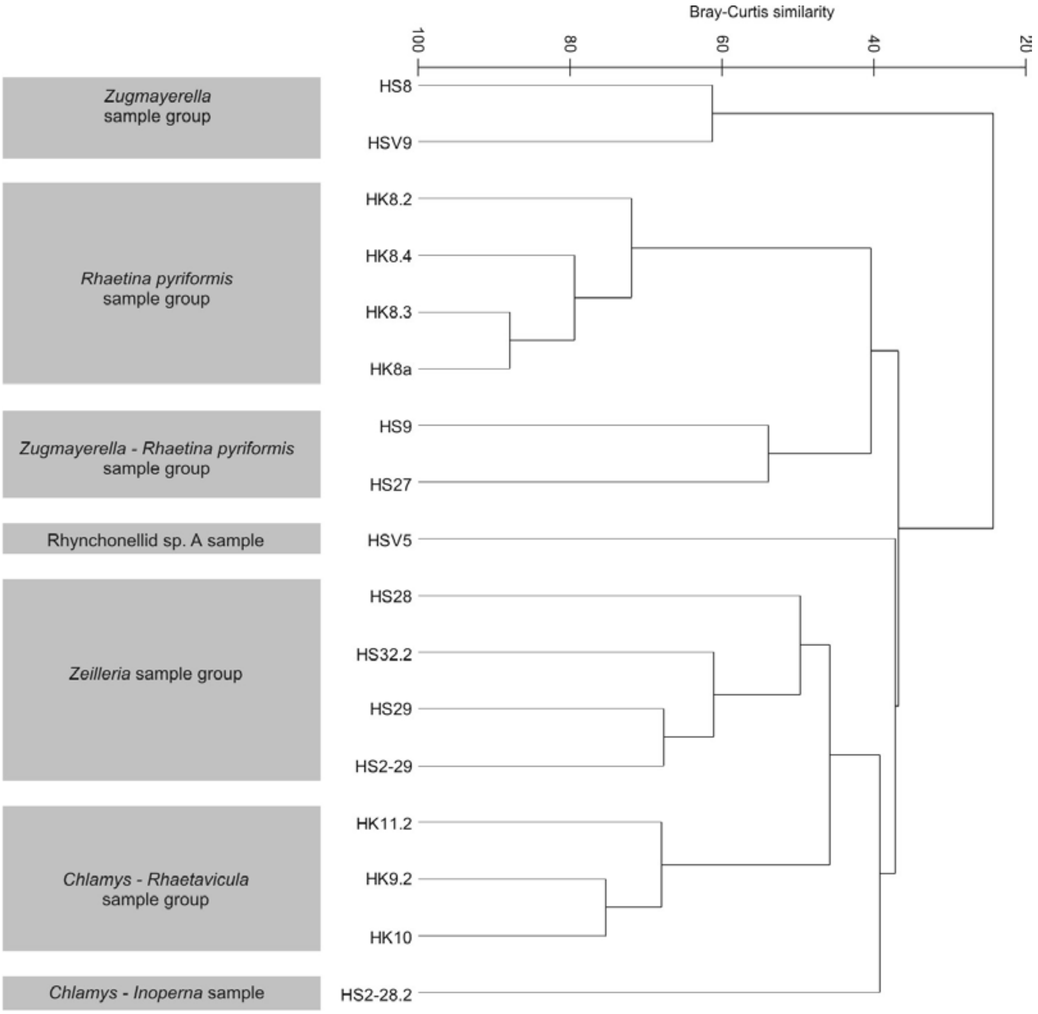


Figure 3 - Q-mode cluster analysis, based on the group-average method and Bray-Curtis similarity, discriminated 5 samples groups and two samples.

(4) The *Zeilleria* sample group is represented by four samples with 484 individuals. The sample-level richness (S) is between 18 and 27, the evenness (PIE) is between 0.86 and 0.94. The pedunculate brachiopods *Zeilleria norica* (19.5%) and *Rhaetina pyriformis* (12.5%) dominate. The endobyssate bivalve *Modiolus hybbensis* (9.8%), and the epibyssate bivalves *Oxytoma (Oxytoma) inequivalvis* (6.8%) and *Chlamys valoniensis* (6.1%) are abundant. Free-lying brachiopods and cementing bivalves are less common. Free-lying, shallow burrowing (*Protocardia rhaetica, Palaeocardita multiradiata*) and deep burrowing bivalves (*Pholadomya* sp., *Pleuromya* sp.) are rare. This group occurs in bioturbated wackestones and floatstones in the middle and upper part of the Šimkovičova section (beds 28, 9, 32.2). The bioclasts are dispersed or loosely packed, poorly sorted and randomly oriented, embedded in micrite rich in calcisiltic bioclastic debris.

(5) Biomicritic wackestone with 61 individuals in the lower part of the Šimkovičova section (bed V5) is dominated by the free-lying brachiopod Rhynchonellid sp. A (27.7%), followed by the epibyssate bivalve *Rhaetavicula contorta* (16.4%) and the pedunculate brachiopods *Zeilleria norica*

(11.5%) and *Rhaetina pyriformis* (11.5%). Endobyssate (4.9%) and free-lying bivalves are less common. One sample with 17 individuals from bed 12 of the Šimkovičova section, not included in the multivariate analyses, is similarly dominated by Rhynchonellid sp. A.

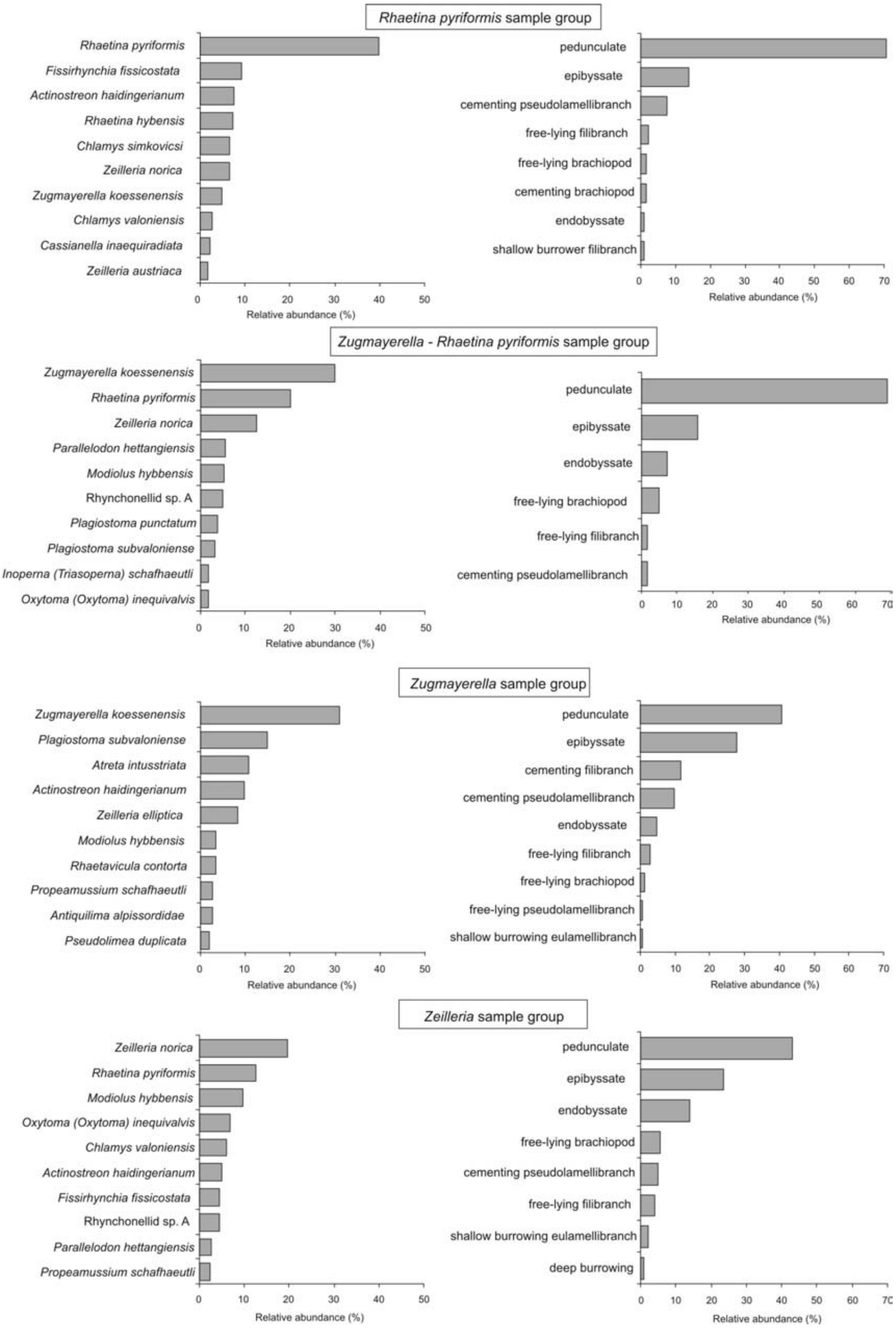


Figure 4 - Relative abundances of the ten most common species and guilds in four brachiopod sample groups.

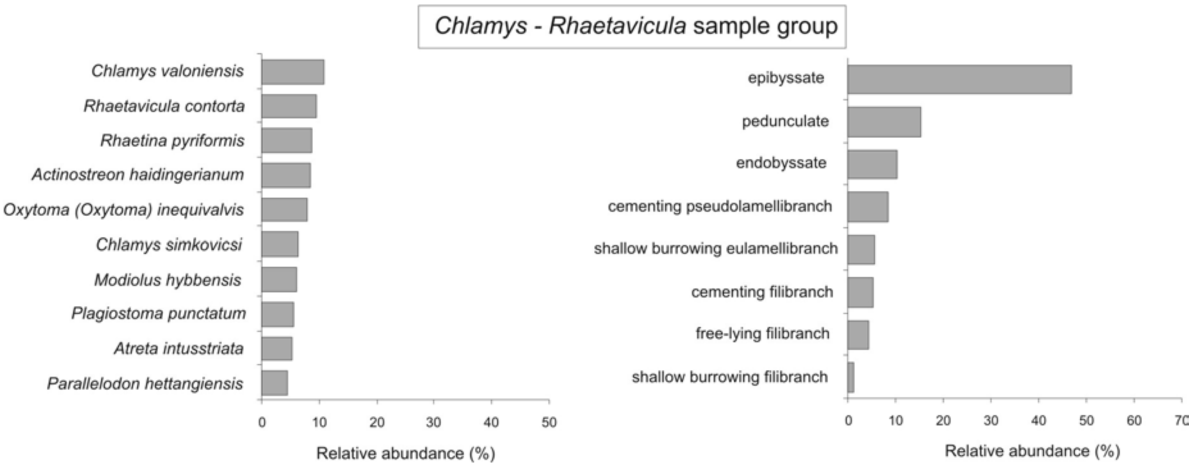


Figure 5 - Relative abundances of the ten most common species and guilds in the sample group dominated by bivalves.

(6) The *Chlamys-Rhaetavicula* sample group is represented by three samples with 298 individuals. The sample-level species richness (S) is between 19 and 28, the evenness (PIE) is very high (between 0.93 and 0.95). The dominant species are the epibyssate bivalves *Chlamys valoniensis* (11%) and *Rhaetavicula contorta* (9.5%), followed by abundant pedunculate brachiopods (*Rhaetina pyriformis*), and cementing (*Actinostreon haidingerianum*, *Atreta intusstriata*), epibyssate (*Oxytoma (Oxytoma) inequivalvis, Chlamys simkovicsi, Plagiostoma punctatum*), and endobyssate bivalves (*Modiolus hybbensis*). Eulamellibranch (5.6%) and filibranch (1.3%) shallow burrowing bivalves are rare. This group is limited to bioclastic-crinoidal marls and marly wackestones with loosely packed, moderately sorted and concordantly oriented bioclasts in the upper part of the Kantorská section (beds 9.2, 10, 11.2).

(7) One sample of biomicritic wackestone from the middle part of the Šimkovičova section with 31 individuals (bed 28.2) is dominated by the epibyssate bivalve *Chlamys valoniensis* (19.4%) and the endobyssate bivalve *Inoperna (Triasoperna) schafhaeutli* (19.4%). Pedunculate and free-lying brachiopods and shallow burrowing bivalves are also abundant. Free-lying and cementing bivalves are rare.

Richness and evenness of brachiopod- and bivalve-dominated samples

The median sampled alpha richness for n = 30 is 14.6 species in bivalve samples and 11.5 species in brachiopod samples (Tab. 2). The median probability of interspecific encounter (PIE) is 0.937 in bivalve samples and 0.827 in brachiopod samples. The median evenness (J) is 0.911 in bivalve samples and 0.787 in brachiopod samples. The samples dominated by bivalves show significantly higher species richness and evenness than the samples dominated by brachiopods (Wilcoxon rank sum test, p = 0.034 for alpha species richness; p = 0.018 for PIE; p = 0.013 for J). The differences in the alpha species richness and PIE are also shown in Figure 6. The highest alpha richness and PIE are represented by bivalve samples of the *Chlamys-Rhaetavicula* sample group and brachiopod samples of the *Zeilleria* sample group. The samples dominated by brachiopod of the *Rhaetina pyriformis* and *Zugmayerella* sample groups show lower levels of the alpha richness and PIE.

	HK8.2	HK8.3	HK8.4	HK8a	HK9.2	HK10	HK11.2	HS8	HSV5	HSV9	HS9	HS27	HS28	HS2-28.2	HS29	HS2-29	HS32.2
Fissirhynchia fissicostata	15	5	9	24	1	5	1	0	2	0	1	0	0	0	8	5	13
Oxycolpella oxycolpos	1	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	6
Rhaetina pyriformis	41	35	37	139	11	7	6	0	7	0	7	5	2	1	15	21	31
Rhaetina hybensis	6	5	13	17	0	0	0	0	3	0	1	0	1	0	2	0	6
Zeilleria norica	10	5	2	27	0	1	0	0	7	0	2	5	8	3	20	46	21
Zeilleria elliptica	2	1	0	3	3	0	0	4	0	8	0	1	3	0	2	1	0
Zeilleria austriaca	2	2	2	3	0	0	0	0	0	0	0	0	0	0	0	1	2
Thecospira haidingeri	1	1	3	4	0	0	1	0	0	0	0	0	0	0	1	0	0
Zugmayerella koessenensis	6	7	2	12	5	6	0	16	1	29	12	6	1	0	0	1	3
Rhynchonellid sp. A	0	1	1	7	0	1	0	2	23	0	2	1	0	3	7	13	6
Austrirhynchia cornigera	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Sinucosta emmrichi	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1
Ostrea anomala	0	0	0	1	0	0	1	1	0	0	0	0	0	1	1	3	0
Actinostreon haidingerianum	4	8	7	34	13	10	3	5	2	9	1	0	5	0	7	1	3
Antiquilima alpissordidae	0	0	2	9	1	4	0	4	0	0	0	0	1	0	1	2	2
Atreta intusstriata	0	0	2	1	5	8	3	11	0	5	0	0	0	0	1	1	1
Plicatula sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Cassianella inaequiradiata	0	2	5	6	5	8	1	0	0	0	0	0	0	0	2	0	8
Chlamys simkovicsi	1	7	9	29	5	5	6	2	1	0	0	0	2	1	2	2	1
Chlamys valoniensis	1	3	4	9	11	16	6	0	1	2	1	0	2	6	6	9	14
Propeamussium schafhaeutli	0	0	0	0	1	0	0	2	0	2	1	0	2	1	2	0	5
Camptonectes sp. n.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0
Pseudolimea duplicata	0	1	0	1	1	2	0	2	0	1	0	0	1	0	1	2	1
Oxytoma (Oxytoma) inequivalvis	1	1	2	6	9	8	5	1	0	1	0	1	2	2	12	16	5
Rhaetavicula contorta	0	0	0	0	9	10	7	5	10	0	0	0	0	0	0	2	1
Pteria (Pteroperna) deshayesi	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0
Inoperna (Triasoperna) schafhaeutli	0	1	1	0	1	2	2	0	0	0	0	1	0	6	9	3	2
Modiolus hybbensis	0	0	0	3	6	10	3	4	3	1	1	2	2	2	24	16	10
Pseudomyoconcha sp.	0	0	0	0	1	2	2	0	0	0	0	0	0	0	1	0	0
Parallelodon hettangiensis	1	0	0	1	3	12	1	0	0	1	0	3	2	0	5	3	0
Trigonia zlambachiensis	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2
Elegantinia inflata	1	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0
Pinna miliaria	0	1	0	0	0	1	0	1	0	1	0	0	2	0	2	0	0
Plagiostoma punctatum	0	1	2	5	4	11	3	0	0	0	0	2	2	0	1	1	2
Plagiostoma subvaloniense	0	0	0	0	0	0	0	13	1	9	2	0	0	0	0	0	0
Myophoricardium sp.	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Nuculana (Nuculana) deffneri	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Trigonucula goniocostata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Pholadomya sp.	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Pleuromya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Palaeocardita multiradiata	0	0	0	0	1	1	2	0	0	0	0	0	0	3	4	0	1
Protocardia rhaetica	0	0	0	0	0	2	0	0	0	0	0	0	1	0	1	1	2
Tutcheria cloacina	0	0	0	0	1	3	3	1	0	0	0	0	0	0	0	0	0

Table 1 - Absolute abundances of brachiopod and bivalves species collected in the Hybe Formation.

To test effects of habitat differences on diversity indices, brachiopod and bivalve samples from the habitats below MSWB are compared (bivalve-dominated samples do not occur in shallower habitats). In this case, differences in the alpha species richness and evenness are insignificant among brachiopod and bivalve samples (Wilcoxon rank sum test, $p = 0.11$ for richness; $p = 0.27$ for PIE; $p = 0.31$ for J). The habitats below MSWB show the highest median PIE (0.92), followed by lower PIE in samples from the habitats below NSWB (0.817) and above NSWB (0.818). The difference among the three habitats is significant both for PIE and J (Kruskal-Wallis test, H = 6.27, p = 0.043 for PIE; H = 6.73, p = 0.035 for J). However, differences among the three habitats in the alpha species richness (n = 30) are insignificant (Kruskal-Wallis test, H = 4.04, p = 0.13). In addition, the difference among carbonates, marly carbonates and marls are significant for PIE, J and alpha species richness (Kruskal-Wallis test, H = 7.54, p = 0.023 for PIE; H = 6.56, p = 0.038 for J; H = 6.2, p = 0.045 for richness). The marls are characterized by the highest median evenness (0.94 for PIE and 0.9 for J) and richness (15 species for n = 30).

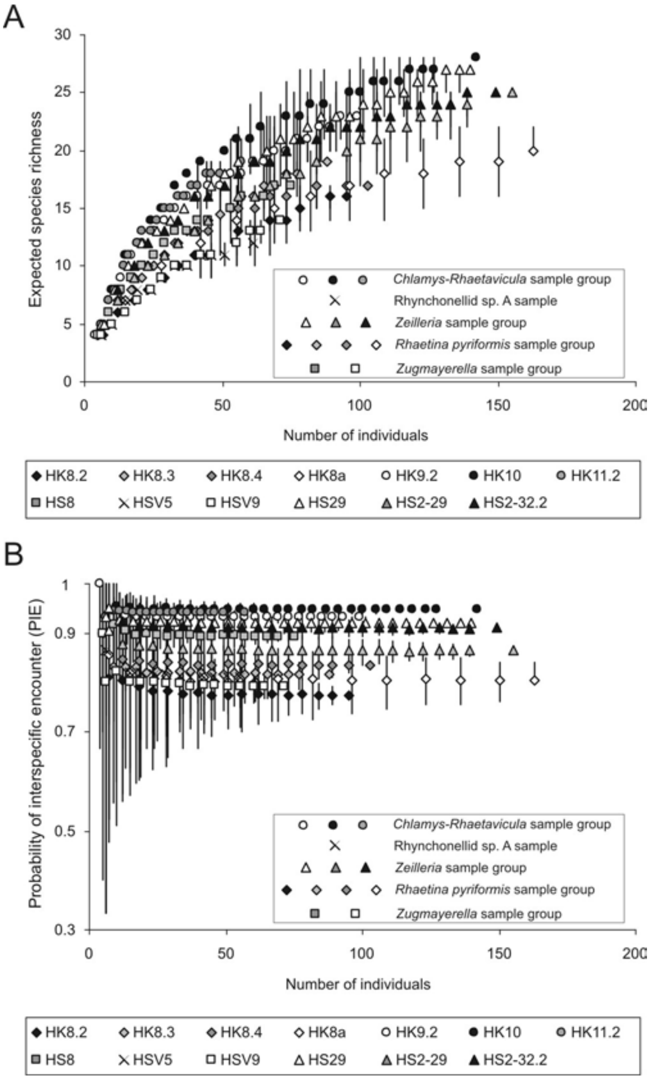


Figure 6 - A. Rarefied sample-level species richness with 95% bootstrapped confidence intervals. For clarity, only some confidence intervals are shown. Only samples with more than 50 individuals are shown. B. Rarefied probability of interspecific encounter with 95% bootstrapped confidence intervals. Only samples with more than 50 individuals are shown.

Sample	Sample group	Number of individuals	Observed species richness	Expected richness (30 individuals)	Shannon-Weaver diversity (H)	Probability of interspecific encounter (PIE)	Pielou evenness (J)
HS2-28.2	*Chlamys-Inoperna*	31	12	11.9	2.29	0.91	0.92
HK9.2	*Chlamys-Rhaetavicula*	99	23	14.3	2.77	0.93	0.88
HK10	*Chlamys-Rhaetavicula*	142	28	16.1	3.00	0.95	0.90
HK11.2	*Chlamys-Rhaetavicula*	57	19	15.0	2.74	0.94	0.93
HSV5	Rhynchonellid sp. A	61	12	9.2	1.95	0.81	0.79
HK8.2	*Rhaetina pyriformis*	95	16	9.4	1.95	0.77	0.70
HK8.3	*Rhaetina pyriformis*	88	19	11.4	2.22	0.82	0.75
HK8.4	*Rhaetina pyriformis*	103	17	11.1	2.24	0.84	0.79
HK8deb	*Rhaetina pyriformis*	344	24	10.6	2.22	0.80	0.70
HS28	*Zeilleria*	40	18	16.0	2.68	0.94	0.93
HS29	*Zeilleria*	140	27	14.0	2.77	0.92	0.84
HS2-29	*Zeilleria*	155	25	11.5	2.42	0.86	0.75
HS32.2	*Zeilleria*	149	25	13.6	2.70	0.91	0.84
HS8	*Zugmayerella*	75	17	12.1	2.42	0.89	0.85
HSV9	*Zugmayerella*	71	14	9.2	1.94	0.79	0.74
HS9	*Zugmayerella-R. pyriformis*	32	12	11.6	1.98	0.82	0.80
HS27	*Zugmayerella-R. pyriformis*	27	10	N.A.	2.08	0.89	0.90

Table 2 - Summary table with several measures of sample-level richness and evenness indices.

Compositional differences among brachiopod- and bivalve-dominated samples

Species composition. Five sample groups discriminated by the cluster analysis show mostly good segregation in NMDS and DCA based on the species composition. Q-mode NMDS based on species composition (Fig. 7A) shows that the samples dominated by brachiopods and epifaunal bivalves do not overlap. The compositional replacement between bivalve- and brachiopod-dominated samples is gradual, with the lowest abundance of bivalves in the *R. pyriformis* sample group, higher abundance of bivalves in the *Zeilleria* and *Zugmayerella* sample groups, followed by their highest abundance in samples dominated by epifaunal bivalves. DCA based on the species composition (Fig. 7B) does not show any segregation of brachiopods and bivalves along the first axis. The sample groups dominated by *Zugmayerella koessenensis* and *Plagiostoma subvaloniense* are separated along the first DCA axis from all other samples (Fig. 7B). The patterns in NMDS and DCA show that the compositional gradient based on species composition is complex and does not directly reflect the simple compositional replacement of samples dominated by brachiopods and epifaunal bivalves. Although the peak abundances of *R. pyriformis, Zugmayerella* and *Zeilleria* are attained in the sample groups in which they dominate, they are common also in other sample groups. The bivalves *Atreta intusstriata* and *Plagiostoma subvaloniense* are more common in brachiopod- than in bivalve-dominated samples. In contrast, *Rhaetavicula* and *Chlamys* are more typical of samples dominated by epifaunal bivalve. Based on abundances of bivalve species only, Q-mode NMDS indicates that brachiopod- and bivalve-dominated samples overlap (Fig. 7E).

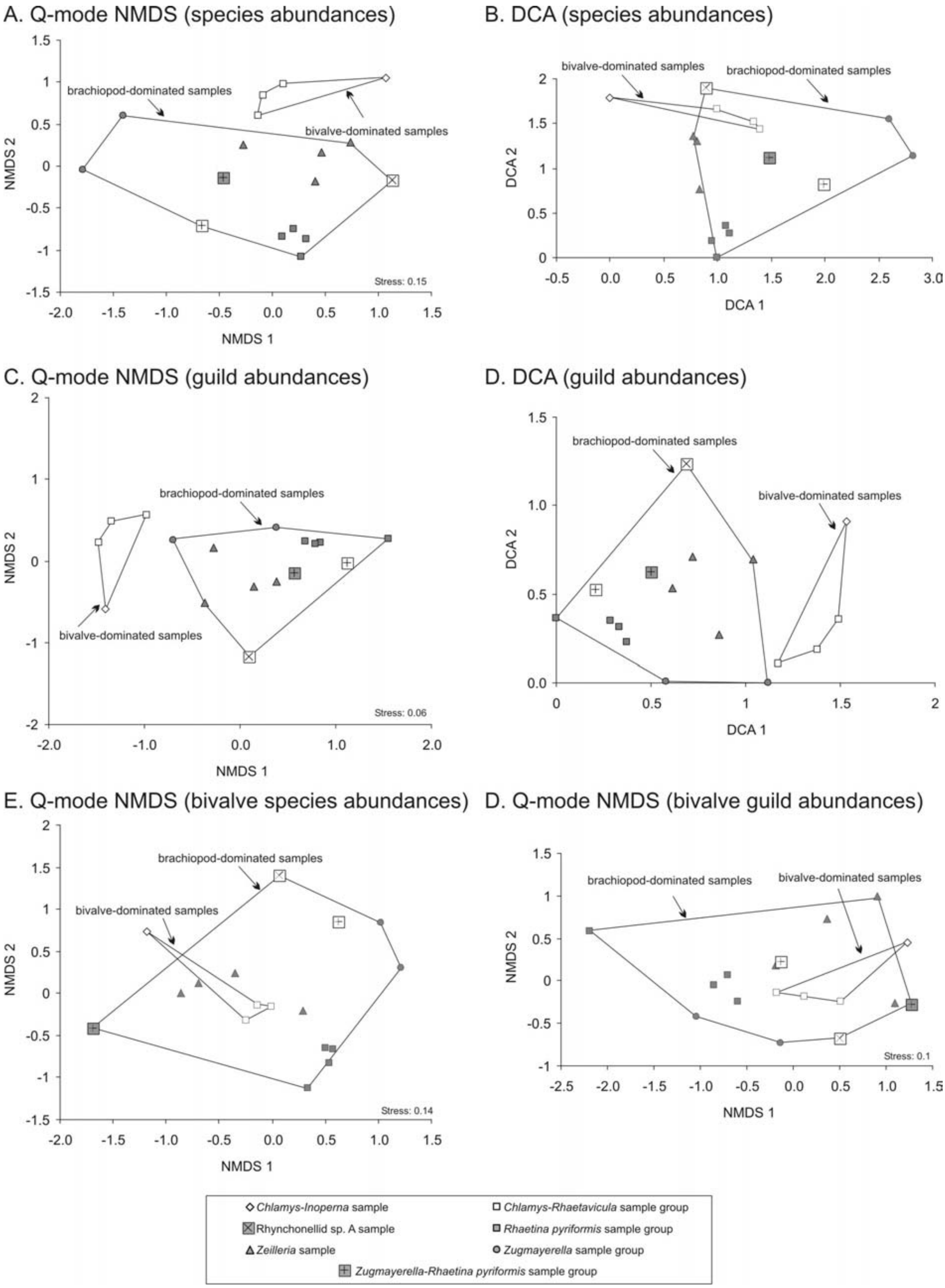


Figure 7 - A. Q-mode non-metric multidimensional scaling (NMDS) based on species abundances. B. Ordination of samples in detrended correspondence analysis (DCA) plot based on species abundances. C. Q-mode NMDS based on guild abundances. D. Ordination of samples in DCA plot based on guild abundances. E. Q-mode NMDS based on abundances of bivalve species only. F. Q-mode NMDS based on abundances of bivalve guilds only.

Guild composition. NMDS of samples based on the guild composition shows a compositional separation of samples dominated by brachiopod and bivalve guilds (Fig. 7C), which are segregated along the first axis in DCA (Fig. 7D). The increase in sample scores along the first DCA axis reflects an increase in abundances of bivalve guilds. The *Zugmayerella* and *Zeilleria* sample groups are more similar to bivalve samples than the *R. pyriformis* sample group because they contain more abundant epibyssate and endobyssate bivalves. The abundance of epibyssate and endobyssate bivalves positively correlates with the increase in sample scores along the first axis. Epibyssate and endobyssate filibranchs are common both in the brachiopod- and bivalve-dominated samples, although their abundance increases towards the latter. Cementing filibranchs were more common in brachiopod- than in bivalve-dominated samples. Shallow burrowing guilds are more common or restricted to samples dominated by epifaunal bivalves. Brachiopod-dominated samples were thus partly characterized by differential abundances of bivalve guild in comparison to samples dominated by epifaunal bivalves. However, based on abundances of bivalve guilds only, Q-mode NMDS indicates that brachiopod- and bivalve-dominated are not substantially segregated (Fig. 7F).

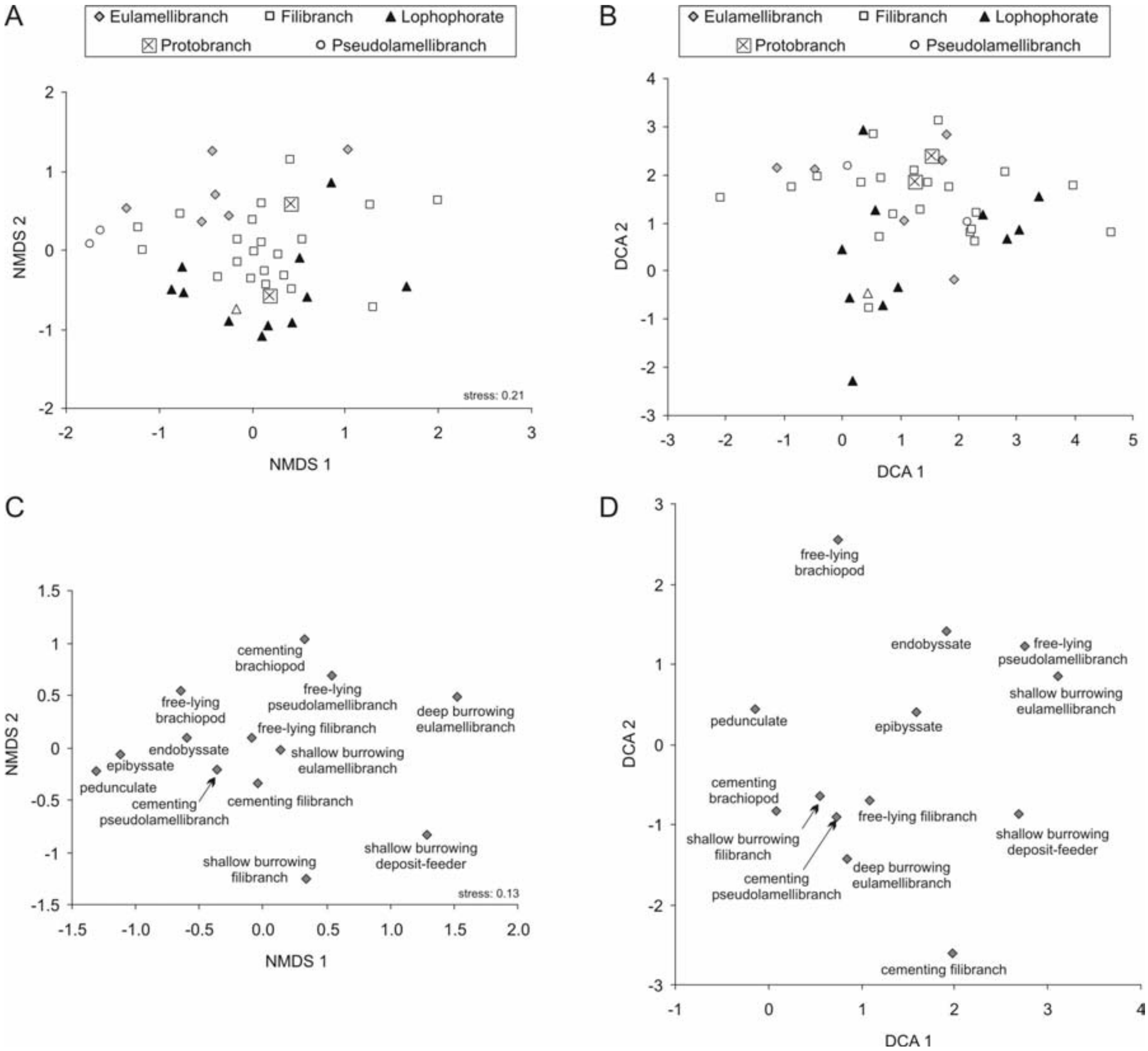


Figure 8 - A. R-mode non-metric multidimensional scaling (NMDS) based on species abundances. Note the separation between particular groups with different feeding strategies. B. Ordination of species in detrended correspondence analysis (DCA) plot based on species abundances. C. R-mode NMDS based on guild abundances. D. Ordination of guilds in DCA based on guild abundances.

Coexistence patterns of brachiopods and bivalves

R-mode NMDS based on species composition (Fig. 8A) shows a rather strong overlap and a low R value between brachiopods and bivalves (ANOSIM, R = 0.125, p = 0.063). In contrast, the differences between guilds are relatively high and significant (Tab. 3). R-mode NMDS based on guild composition (Fig. 8C) demonstrate that brachiopod guilds co-existed more commonly with epibyssate and endobyssate filibranchs and cementing pseudolamellibranchs than with infaunal eulamellibranch and protobranch guilds. DCA based on species abundances shows a rather poor separation between brachiopods and bivalves, and among guilds with different feeding strategies (Fig. 8B). However, the pattern visible in DCA based on guild abundances shows that the pedunculate brachiopods have the lowest guild scores along the first axis, followed by free-lying brachiopods, filibranchs and cementing pseudolamellibranchs. Free-lying pseudolamellibranchs and shallow burrowing eulamellibranchs and protobranchs have the highest guild scores (Fig. 8D).

To simplify the comparison of the guilds, only guilds that are represented by more than three species were tested with R-mode based ANOSIM (i.e., pedunculate brachiopods, epibyssate and endobyssate filibranchs and shallow burrowing eulamellibranchs) because low species number limits reliability of an R value and estimation of its significance level (Tab. 3). R-mode based ANOSIM thus tests differences (1) among these four guilds, (2) among five guilds with distinct feeding strategies (i.e., brachiopods, filibranchs, pseudolamellibranchs, and eulamellibranchs), and (3) among four guilds with distinct substrate strategies (i.e., epifaunal, semi-infauna, and infaunal bivalves, and brachiopods). Brachiopods and eulamellibranch bivalves (R = 0.41, p = 0.001) significantly differ in sample-level relative abundances. The difference between filibranchs and brachiopos (R = 0.13, p = 0.04) and filibranchs and eulamellibranchs (R = 0.195, p = 0.078) is lower and of borderline significance. Epifaunal brachiopods and infaunal bivalves (R = 0.45, p < 0.0001) and epifaunal bivalves and infaunal bivalves (R = 0.395, p < 0.0001) significantly differ in sample-level relative abundances. The difference between epifaunal brachiopods and bivalves is of borderline significance (R = 0.123, p = 0.029).

R-mode based one-way ANOSIM testing between-guild differences in abundance patterns	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Substrate categories (guilds with more than two species)				
Global test	0.122	0.062	10000	623
pedunculate, epibyssate	0.086	0.099	10000	990
pedunculate, endobyssate	0.147	0.171	715	122
pedunculate, shallow burrowing	0.525	0.004	715	3
epibyssate, endobyssate	-0.09	0.659	1365	900
epibyssate, shallow burrowing	0.184	0.146	1365	199
endobyssate, shallow burrowing	-0.156	0.771	35	27
Simplified substrate categories				
Global test	0.235	0.0001	10000	1
Brachiopod epifauna, Epifauna	0.123	0.029	10000	287
Brachiopod epifauna, Semi-infauna	0.053	0.352	1820	640
Brachiopod epifauna, Infauna	0.446	<0.0001	10000	0
Epifauna, Semi-infauna	-0.03	0.53	5985	3175
Epifauna, Infauna	0.395	<0.0001	10000	0
Semi-infauna, Infauna	0.066	0.317	1001	317
Feeding strategies				
Global test	0.193	0.005	10000	47
Brachiopods vs. filibranchs	0.13	0.04	10000	401
Brachiopods vs. eulamellibranchs	0.41	0.001	10000	11
Filibranchs vs. eulamellibranchs	0.195	0.083	10000	831

Table 3 - Results of analysis of similarities (ANOSIM), which tests differences in species abundance among brachiopods and bivalve guilds. The alpha value for pairwise comparisons adjusted with the Bonferroni correction is 0.016 (0.05/3).

Compositional differences among habitats

(1) The differences in sample-level composition among habitats above NSWB, below NSWB and below MSWB are significant both for species ($R = 0.6$, $p < 0.0001$) and guilds ($R = 0.25$, $p = 0.035$, Tab. 4). The compositional differences demonstrate that samples dominated by brachiopods and epifaunal bivalves were separated along the bathymetric gradient. Habitats above NSWB were dominated by *Zugmayerella koessenensis* and *Plagiostoma subvaloniense*, habitats below NSWB by *Rhaetina pyriformis* and *Fissirhynchia fissicostata*, and habitats below MSWB by *Zeilleria norica, Rhaetina pyriformis* and bivalves (Fig. 9A). In addition, three pairwise comparisons give high and significant between-habitat differences in species composition (Tab. 4). In terms of guild composition, habitats above MSWB are dominated by pedunculate brachiopods, followed by epibyssate filibranchs and cementing pseudolamellibranchs. Epibyssate bivalves, however, dominate in habitats below MSWB, followed by less common pedunculate brachiopods and endobyssate bivalves (Fig. 9B). Pairwise comparisons based on guild composition show that the compositional difference between habitats below NSWB and below MSWB is relatively high and significant (Tab. 4).

(2) Effects of substrate consistency on composition of benthic communities are shown by relatively high and significant differences among the four substrate types based both on species ($R = 0.72$, $p < 0.0001$) and guild composition ($R = 0.48$, $p = 0.0005$, Tab. 4). The compositional differences based on guild composition between floatstones/packstones and mudstones/wackestones in the carbonate-rich deposits are rather low, with pedunculate brachiopods and epibyssate bivalves dominating in both substrate types (Fig. 10). The compositional differences based on guild composition between floatstones and wackestones in marl-rich deposits are higher. The decrease in substrate firmness, consistency and grain size in marl-rich deposits correlates with the increase in abundance of bivalve guilds and the decrease in abundance of brachiopods (Fig. 10).

(3) Effects of terrigenous vs. carbonate sedimentation on differential distribution of brachiopods and bivalves are indicated by differences in species ($R = 0.28$, $p = 0.016$) and guild composition ($R = 0.38$, $p = 0.007$) among marls, marly carbonates and carbonates. Marl-rich habitats are represented by the *Chlamys-Rhaetavicula* sample group only, which is dominated by epibyssate bivalves (*Rhaetavicula, Chlamys, Oxytoma*), pedunculate brachiopods (*R. pyriformis*), cementing bivalves (*Actinostreon haidingerianum*) and endobyssate bivalves (*Modiolus hybbensis*) (Fig. 11). Marly carbonates and carbonates are dominated by pedunculate brachiopods and epibyssate bivalves (Fig. 11). Based on guild composition, the pairwise differences between marls on one hand and marly carbonate and carbonates on the other are relatively high and significant (Tab. 4). Brachiopod- and bivalve-dominated communities were separated thus also separated along the gradient that reflects variation in terrigenous supply. Brachiopods dominated in habitats with lower terrigenous supply and abundance of bivalves increased towards habitats with higher terrigenous supply.

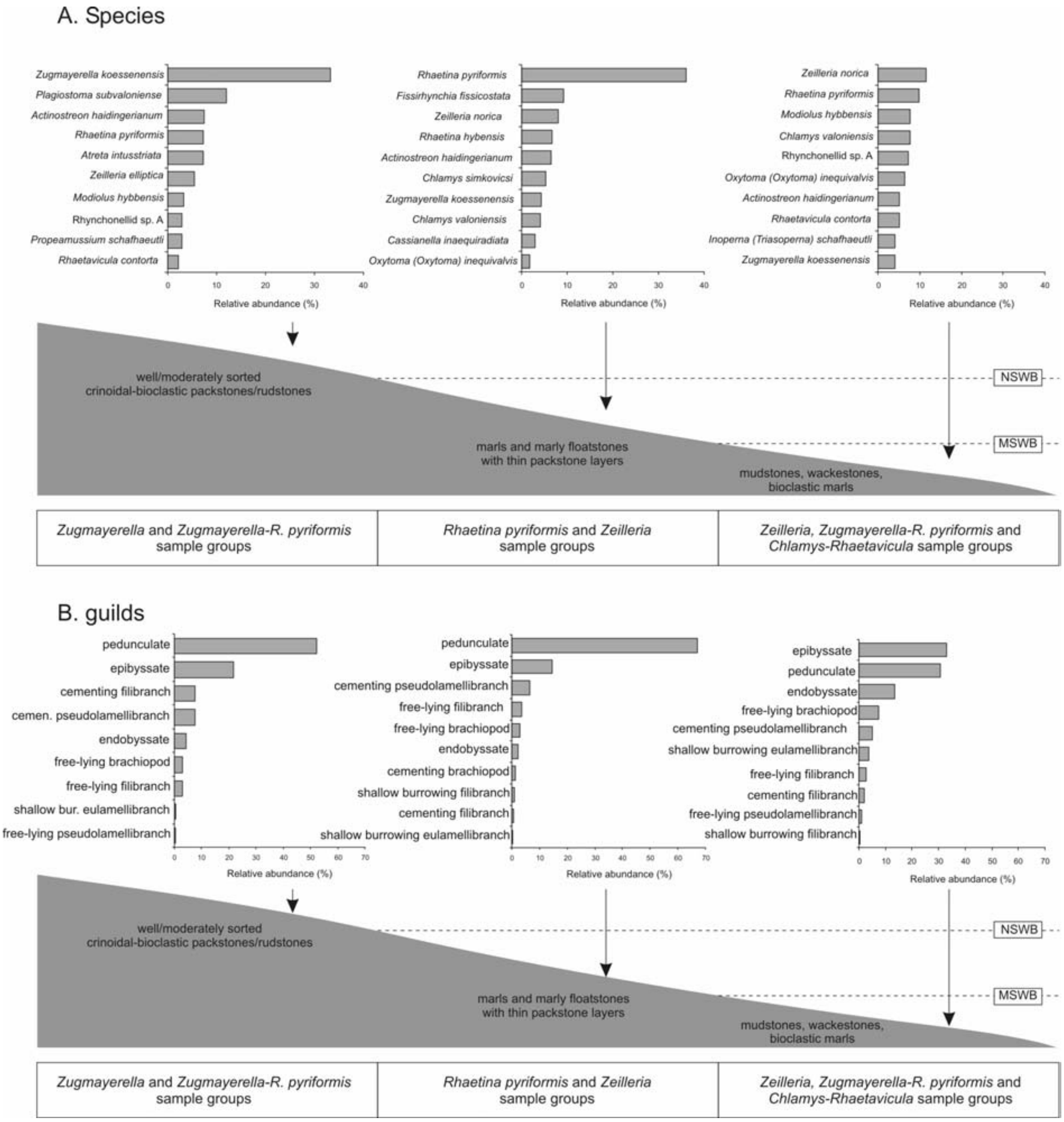


Figure 9 - Distribution of brachiopod and bivalve species and guilds along an onshore-offshore gradient. A. Species. B. Guilds.

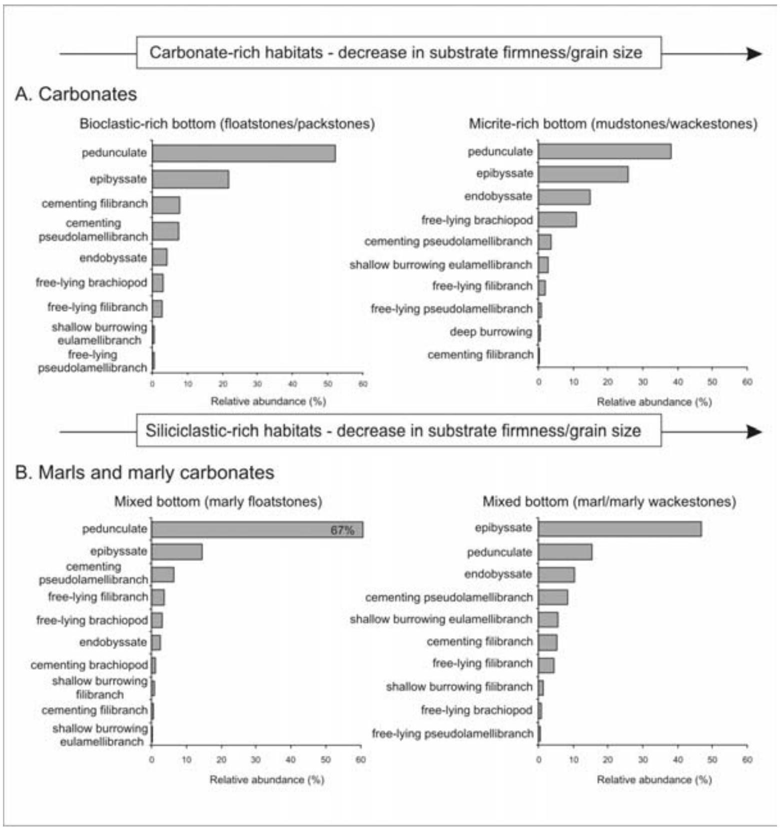


Figure 10 - Distribution of brachiopod and bivalve guilds along a gradient with varying substrate properties. A. Carbonate-rich habitats. B. Marl-rich habitats.

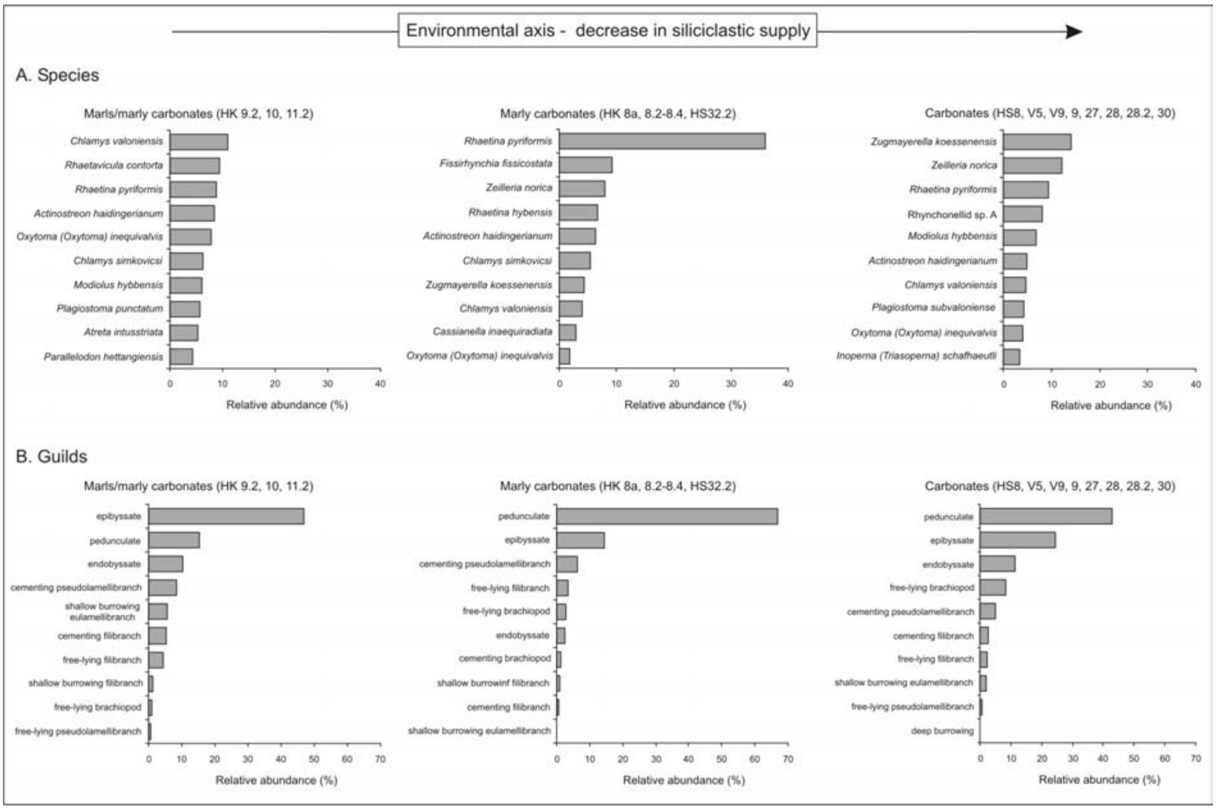


Figure 11 - Distribution of brachiopod and bivalve species and guilds along a gradient with varying terrigenous supply. A. Species. B. Guilds.

	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Species - wave-base level				
Global test	0.6	<0.0001	10000	0
Below NSWB, Below MSWB	0.442	0.001	2002	3
Below NSWB, Above NSWB	0.959	0.018	56	1
Below MSWB, Above NSWB	0.73	0.005	220	1
Guilds - wave-base level				
Global test	0.245	0.035	10000	353
Below NSWB, Below MSWB	0.42	0.0099	2002	20
Below NSWB, Above NSWB	0.067	0.339	56	19
Below MSWB, Above NSWB	0.088	0.282	220	62
Species - marls vs. limestones				
Global test	0.28	0.016	10000	155
marly carbonate, mixed	1	0.018	56	1
marly carbonate, carbonate	0.268	0.049	2002	98
mixed, carbonate	0.071	0.309	220	68
Guilds - marls vs. limestones				
Global test	0.38	0.07	10000	73
marly carbonate, mixed	1	0.018	56	1
marly carbonate, carbonate	0.086	0.219	2002	439
mixed, carbonate	0.423	0.018	220	4
Species - substrate consistency				
Global test	0.715	<0.0001	10000	0
Guilds - substrate consistency				
Global test	0.483	0.0005	10000	5

Table 4 - Results of analysis of similarities (ANOSIM), which tests differences in species and guild composition among habitats differing in the wave-base level, terrigenous/carbonate supply, and substrate consistency. The alpha value for pairwise comparisons adjusted with the Bonferroni correction is 0.016 (0.05/3).

Discussion

(1) The differences in alpha species richness and evenness between samples dominated by brachiopods and bivalves may indicate inherent differences in diversity structure between brachiopod- and bivalve-dominated communities. However, these differences are probably also related to environmental effects because habitats below MSWB show higher median evenness than shallower habitats, and marlk-rich habitats show higher median evenness and richness than carbonate-rich habitats.

(2) The difference in abundance patterns between guilds as measured by the R values point to the differential habitat requirements of brachiopod and bivalve guilds. The preferential co-existence of brachiopods with filibranch and pseudolamellibranch, mostly epifaunal bivalves, than with eulamellibranch, mostly infaunal bivalves, is in accord with the actualistic prediction about their differential autecology (Rhodes and Thompson, 1993). This prediction indicates that brachiopods have similar habitat requirements with filibranch and pseudolamellibranch bivalves with respect to substrate (both are mostly epifaunal) and food supply (both can tolerate reduced food supply). Both groups are able to cope with low nutrient supply because brachiopods have low metabolic demands (Peck et al., 1989, 2005), and filibranch and pseudolamellibranch bivalves have high clearance rates.

(3) Between-habitat compositional differences and separation of samples dominated by brachiopods and epifaunal bivalves also imply their different environmental preferences. Although the environmental and compositional gradient is shorter when compared to the benthic communities of the coeval Kössen Formation of the Eastern Alps (e.g., communities dominated by infaunal bivalves do not occur in the Hybe Formation), the replacement pattern between brachiopods and bivalves with respect to their environmental distribution show some similarities and differences when the two formations are compared (Chapter 3; Tomašových, 2006b). In general, brachiopods are most common in shallow, mixed-bottom habitats above MSWB, and bivalves increase in abundance towards deep, soft-bottom habitats below MSWB. The higher abundance of bivalves in deep-water habitats of the Hybe Formation contrasts with the higher abundance of brachiopods in deep-water habitats of the Kössen Formation.

(4) The compositional separation between soft-bottom habitats dominated by epifaunal bivalves and mixed-bottom habitats dominated by brachiopods holds true for terrigenous-rich conditions only. Although substrate variations can partly explain the preferential co-existence of brachiopods and epifaunal bivalve guilds (Kidwell and Jablonski, 1983), the dominance of brachiopods in highly bioturbated mudstones and wackestones (*Zeilleria* sample group) hints at their success in soft-bottom habitats. This distribution pattern implies that the replacement between brachiopod and bivalve samples cannot be explained by the substrate variations only. Although differential preservation and sampling artifacts can cause under-representation of originally aragonitic bivalves in soft-bottom habitats, the main compositional difference is between brachiopod samples on one hand and samples with bivalves with calcitic or mixed shell structure on the other. The presence of well preserved, originally aragonitic bivalves in the *Zeilleria* sample group also implies that differential preservation and sampling alone did not lead to over-representation of brachiopods in soft-bottom habitats. The high abundance of *Zeilleria norica* in soft-bottom, carbonate-rich habitats might be enhanced by some factors that inhibited infaunal bivalves. Infaunal bivalves can be limited by decreased flow velocities and decresed oxygen levels that can arise in semi-closed basins or embayments during relative seal level rise.

(4) The role of varying terrigenous and land-derived nutrient supply is indicated by differences between marl-rich and carbonate-rich habitats. When habitats differing in the terrigenous supply are compared, carbonate-rich habitats below MSWB were mainly dominated by pedunculate brachiopods, and less commonly by epibyssate and endobyssate bivalves (*Zeilleria norica* sample group). Marl-rich habitats below MSWB were dominated by epibyssate bivalves, and by less common brachiopods, endobyssate and infaunal bivalves (*Chlamys-Rhaetavicula* sample group). In general, brachiopods were thus more common in carbonate-rich habitats and bivalves in marl-rich habitats. This result is similar to that observed in the Kössen Formation (Chapter 3; Tomašových, 2006b). Lower abundance of brachiopods and higher abundance of eulamellibranch bivalves in marl-rich habitats are in accord with the actualistic hypotheses that brachiopods are inhibited by too high particle concentrations and eulamellibranch bivalves can be limited by low nutrient supply conditions. The higher abundance of brachiopods and lower abundance of bivalves in carbonate, nutrient-poor habitats was observed also in the Lower Jurassic deposits of France and Spain (Fürsich et al., 2001; Gahr, 2005) and the Upper Jurassic deposits of India (Fürsich et al., 2004a, b). The difference in turbidity and nutrient supply, partly driven by variations in siliciclastic supply can thus explain compositional differences between brachiopod and bivalve samples and abundance of brachiopods in carbonate-rich, soft-bottom habitats of the Hybe Formation.

Conclusions

The formation-level analyses based on 17 samples from mixed, marl-carbonate deposits of Late Triassic age demonstrate differences in community structure between samples dominated by brachiopods and epifaunal bivalves. Brachiopods and bivalves show differential co-existence patterns and differ in environmental distribution. Brachiopods co-occur more commonly with epifaunal, filibranch and pseudolamellibranch bivalves, than with infaunal, eulamellibranch and protobranch bivalves. Relatively high and significant differences among habitats differing in the wave-base level, in the terrigenous supply, and in the substrate consistency poin to the role of physical factors in determining distribution patterns of brachiopods and bivalves. Brachiopods are common in shallow, carbonate-rich habitats with bioclastic bottom. Bivalves increase in abundance towards deep, terrigenous-rich habitats with soft-bottom conditions. On one hand, the increased terrigenous supply leading to higher turbidity levels, and possibly also to higher sediment-mediated biological disturbance due to higher abundance of infaunal bivalves, might be responsible for the decreased abundance of brachiopods in the terrigenous-rich habitats. On the other hand, the increased terrigenous supply might correlate with higher land-derived nutrient input that is beneficent for food supply requirements of infaunal bivalves. This study stresses the role of physical changes in determining brachiopod and bivalve distribution patterns, possibly coupled with more intense biotic interactions, because brachiopods and bivalves differ in their preferences with respect to sedimentation and nutrient supply regime. Local community replacements in the Hybe Formation thus give support for the role of physical perturbations related to variations in terrigenous supply in biotic transition between brachiopod- and bivalve-dominated samples.

6. Evaluating compositional turnover of brachiopod communities during the end-Triassic mass extinction (Northern Calcareous Alps): removal of dominant groups, recovery and community re-assembly

(with Miloš Siblík)

Abstract. This study highlights the role of large-scale physical perturbations in mediating biotic replacements and shows that an environmental disturbance at the Triassic/Jurassic boundary correlates with abrupt and substantial changes in composition of brachiopod communities. It changed a phylogenetic structure of Early Jurassic brachiopod communities owing to a removal of higher taxa that were abundant in the Late Triassic. A replacement of brachiopod communities since the Early up to the Late Rhaetian related to a combination of habitat tracking and immigration/local extinction events indicates a high compositional turnover in the Kössen Basin (Northern Calcareous Alps). This turnover is of local nature only because Early Rhaetian communities migrated or tracked their habitats beyond the Kössen Basin and persisted up to the Late Rhaetian in other regions. A several meters thick siliciclastic interval with rare brachiopods at the base of the Hettangian marks the extinction-survival interval. This interval is coeval with a negative carbon isotope anomaly, implying a correlation with global perturbation of carbon cycle. A rapid brachiopod recovery is indicated by a presence of several distinct communities in late Early and Middle Hettangian that show onshore-offshore differentiation and beta diversity comparable to pre-extinction levels. Analyses of similarities demonstrate that (1) the compositional turnover of brachiopod communities on generic level at the Triassic/Jurassic boundary (TJB) (R = 0.83) is substantially higher than turnovers between the Rhaetian zones (R = 0.28-0.57) and between the Hettangian zones (R = 0.28-0.53), and (2) the turnover on superfamily level at the TJB accounts for differential composition of Rhaetian and Hettangian communities. A global extinction of athyridoid, spondylospiroid and dielasmatoid superfamilies characterized by high-community level abundances during the Late Triassic led to new assembly of Jurassic brachiopod communities from surviving superfamilies. In addition to persisting rhynchonellids and zeillerioids, Hettangian brachiopod communities were dominated by terebratuloids, spiriferinoids and pennospiriferinoids. These superfamilies were characterized in the Late Triassic by low community-level abundance. We argue for tracking the phylogenetic structure of communities across mass extinction events because measuring the turnover in community-level abundance of higher taxa can be highly relevant for estimating ecologic impact of mass extinctions. Taxonomic extinction rate metrics or diversity measures can be depressed by surviving taxa that do not re-attain their pre-extinction community-level abundance.

Introduction

One of the main interests in analysing variations in diversity, extinction rates, extinction selectivity, community attributes and morphologic disparity across mass extinctions is to assess the effects of environmental disturbances on evolutionary pathways and ecology, and to understand how ecosystems respond to large-scale environmental perturbations (Erwin, 2001). In the last years, a strong emphasis is ascribed to ecologic changes during mass extinctions (Droser et al., 1997; Harries et al., 1996; Harries and Little, 1999; Lockwood, 2003; Hansen et al., 2004; Kiessling and Baron-Szabo, 2004; McGhee et al., 2004; Twitchett et al., 2004). These analyses indicate that effects of mass extinctions are more diverse and complex than indicated by taxonomic extinction metrics at boundary intervals (Jablonski, 2002). One of the most profound effects is that mass extinctions remove successful incumbents (Rosenzweig and McCord, 1991; Jablonski, 2001). Extensive environmental perturbations leading to mass extinctions thus have a strong impact on evolutionary trajectories because taxonomic survivorship may differ from that operating during "background" times.

In this study, to evaluate the effects of environmental perturbation on brachiopod ecology at the end of the Triassic, a compositional turnover as the change in species composition and relative abundances across the Triassic/Jurassic boundary (TJB) is analyzed. To exclude biogeographic effects, the study area is restricted to the intra-platform Kössen Basin (Northern Calcareous Alps, NCA). This basin was situated in the western margin of the Tethys Ocean in the Late Triassic (Fig. 1). The area of the NCA is one of the few places in the world where both Rhaetian and Hettangian brachiopods are numerically common. In addition, biostratigraphic correlations of Rhaetian and Hettangian sections are constrained by ammonites and conodonts in the NCA, allowing their subdividing up to the zone levels. This study is of dual significance. First, because the Mesozoic represents a transition interval when the "Paleozoic" evolutionary fauna was replaced by the "Modern" evolutionary fauna (Sepkoski, 1996; Alroy, 2004), distinguishing the role of mass extinctions vs. background times in forcing this replacement is of high importance (Miller, 1998; Chen et al., 2005). Second, this study is one of the first attempts to assess the impact of the end-Triassic mass extinction on Rhaetian and Hettangian brachiopods in terms of their distribution patterns and environmental preferences on zone level.

Two inter-related hypotheses are tested here. First, there is a difference in the composition of pre- and post-extinction brachiopod communities in terms of community-level abundance of brachiopod taxa. In order to avoid bias due to habitat tracking, local immigration/extinction and pseudo-extinction, this hypothesis is evaluated within spatial framework and on several taxonomic levels. Second, environmental preferences of pre- and post-extinction brachiopod taxa are different. This second hypothesis is related to an idea of Sandy (1995). He compared distribution patterns Middle-Late Triassic and Early Jurassic brachiopods and invoked a change in environmental preferences of brachiopod suborders/orders at the TJB.

Rhaetian and Hettangian deposits with brachiopods in the NCA

Rhaetian deposits. Brachiopods analysed in this study are derived from the Kössen Formation, which consist of the Hochalm Member and the Eiberg Member, from the "Oberrhät" Limestone and the Starhemberg Limestone. In the Frankenfels Nappe of the Bajuvaric Unit, the upper part of the Kössen Formation is represented by the Restental Member (Golebiowski, 1990). Golebiowski (1990) subdivided the Kössen Formation into eight stratigraphic units (Fig. 2). The general environmental history of the Kössen Basin is interpreted as a response to a relative sea level rise (i.e., from a shallow lagoon in the Early Rhaetian up to an intra-platform basin at the end of the Rhaetian, Kuss, 1983; Golebiowski, 1991; Holstein, 2004). The lowermost part of the Hochalm Member (Unit 1) is formed by carbonates of shallow subtidal and peritidal origin. It contains no brachiopods. The first brachiopods occur in Unit 2 that consists of small-scale sequences composed of the siliciclastic and carbonate intervals (Fig. 3A; Golebiowski, 1990; Satterley, 1996, Tomašových, 2006b). Monospecific brachiopod assemblages with *Rhaetina gregaria* are limited to the carbonate intervals and lowermost part of the siliciclastic intervals (Fig. 3A). Signs of storm reworking represented by high-energy sedimentary features and storm-reworked shell beds indicate habitats between fair-weather wave base and maximum storm wave base (MSWB). In Unit 3, thick, laterally extensive marlstone interval onlaps onto the carbonate platform and marks the maximum deepening event in the Early Rhaetian (Golebiowski, 1990). A regular alternation of biomicritic limestones and marlstones is typical of this unit. Unit 4 is characterized by a widespread development of coral beds and initial formation of large-scale patch-reefs (Fig. 3B). The Eiberg Member is characterized by a cyclic alternation of marlstones, marly limestones and micritic limestones, which record habitats below MSWB (Fig. 3C).

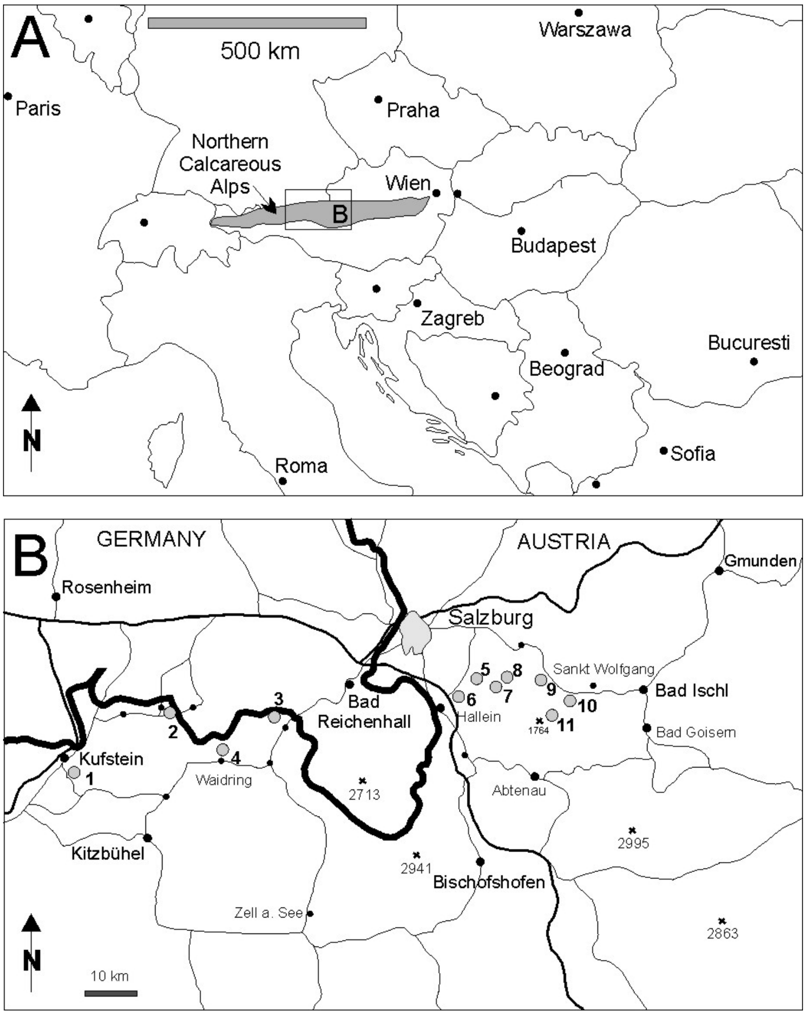


Figure 1 - (A) Geographic position of the Northern Calcareous Alps. (B) Geographic position of Rhaetian and Hettangian sections between Kufstein and Bad Ischl. Some of these sections are shown in Figures 4 and 6. 1 – Eiberg (Rhaetian-Hettangian), 2 – Kössen – Weissloferbachgraben (Rhaetian), 3 – Hochalm – Sonntagshorn (Rhaetian), 4 – Steinplatte (Rhaetian-Hettangian), 5 – Gaissau – Mörtlbachgraben (Rhaetian), 6 – Adnet (Rhaetian-Hettangian), 7 – Hochleitengraben (Hettangian), 8 – Rötelwand (Rhaetian), 9 – Saubachgraben (Hettangian), 10 – Breitenberg (Hettangian), 11 – Kendlbachgraben (Rhaetian-Hettangian).

The Restental Member is a stratigraphic equivalent of the Eiberg Member. It originated in a shallow restricted basin with uniform, siliciclastic-rich deposition. Importantly, taxa and some communities typical of the Hochalm Member (e.g., *Zugmayerella* community) persist here up to the Upper Rhaetian (Golebiowski, 1990). The "Oberrhät" Limestone is formed by patch-reefs with scleractinians, sphinctozoans and diverse bioclastic debris (Stanton and Flügel, 1989). The patch-reefs corresponding to habitats above MSWB laterally replace the Eiberg Member. They are either in intra-basinal or in marginal, basin-platform boundary position. The Starhemberg Limestone forms layers within the Dachstein Limestone in the Tirolic and Juvavic units.

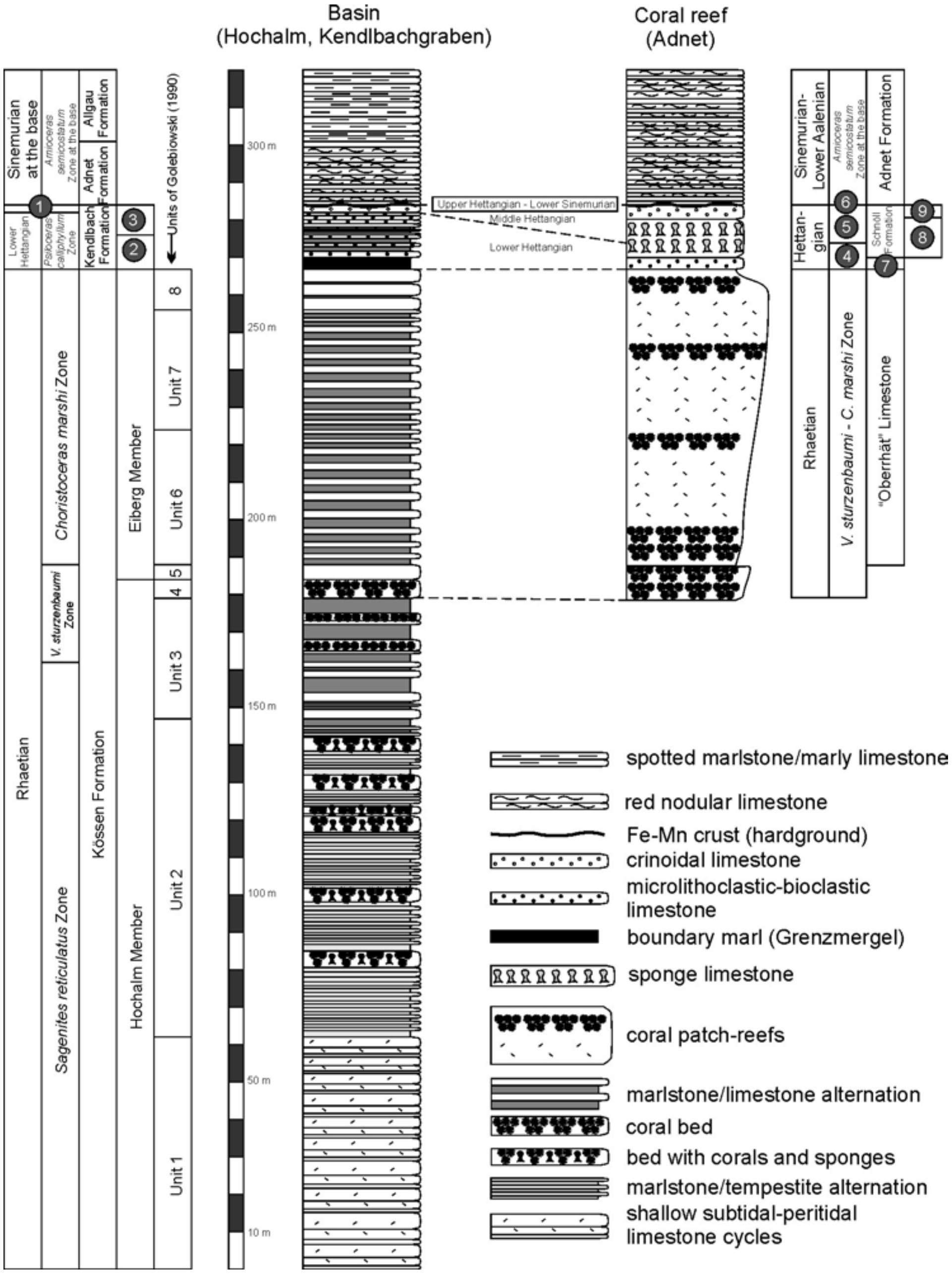


Figure 2 – A composite section across the Triassic/Jurassic boundary (TJB) in the Northern Calcareous Alps. Bio- and lithostratigraphic subdivisions of Rhaetian and Hettangian follow Golebiowski (1990), Böhm (2003) and Böhm et al. (1999). Note that lithostratigraphic units within the Kössen Formation were re-numbered from 1 to 8 (in contrast to four units within the Hochalm Member and four units within the Eiberg Member). 1 – The condensed zone encompasses the Middle-Upper Hettangian (*K. megastoma* and *A. marmoreum* zones) and lowermost Sinemurian. 2 – The Tiefengraben Member, at the base with the boundary marl (Grenzmergel). 3 – The Breitenberg Member, in the uppermost part with the Enzesfeld Limestone. 4 – *P. calliphyllum* Zone (Lower Hettangian). 5 – *K. megastoma* Zone (Middle Hettangian). 6 – The condensed zone encompassing most probably the Upper Hettangian and lowermost Sinemurian (*A. marmoreum* Zone). 7 – The Kendlbach Formation. 8 – The Langmoos Member. 9 – The Guggen Member. The simplified section of the Kössen Basin is based on the Hochalm (Rhaetian part) and Kendlbach sections (Hettangian part). The simplified section of the Adnet is based on the Schnöll Quarry.

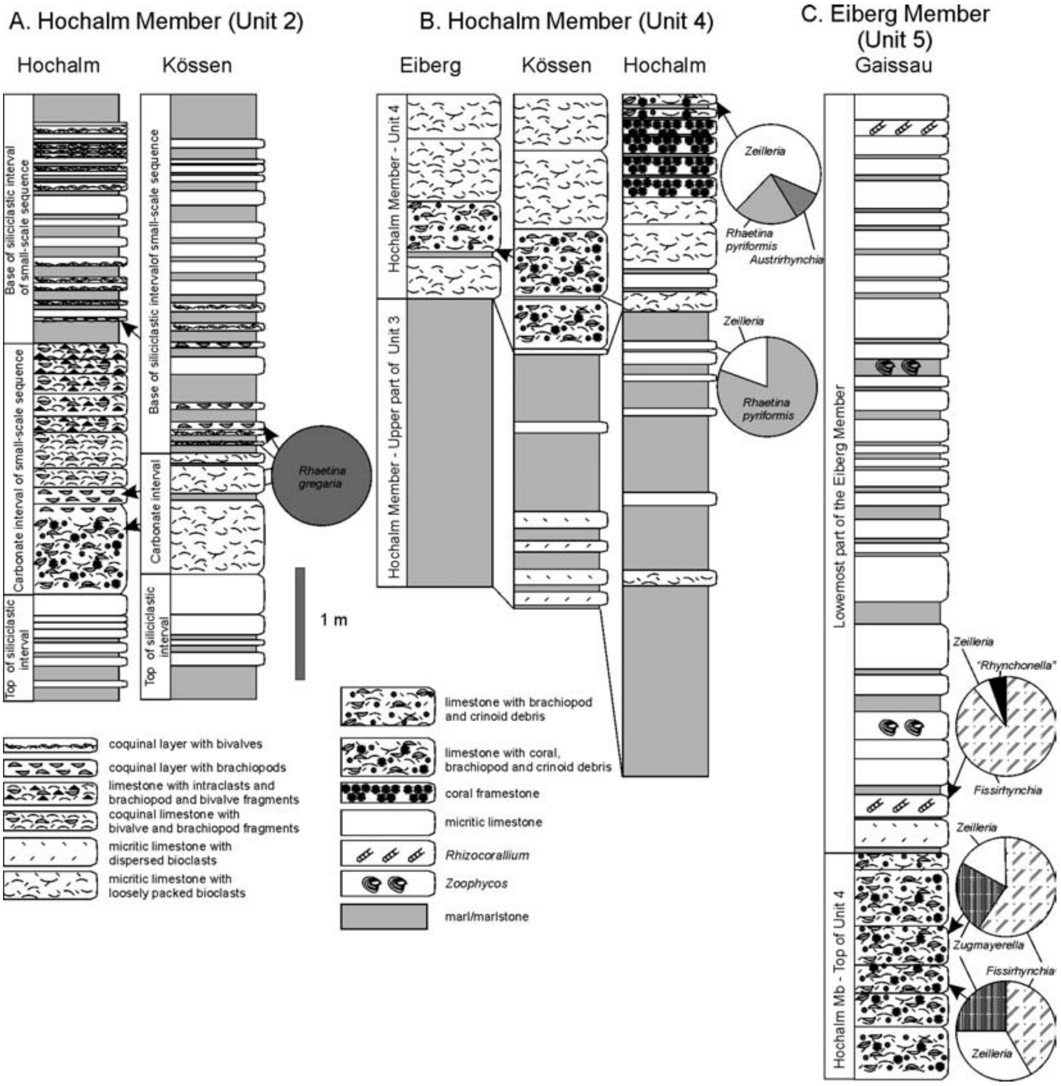


Figure 3 - Stratigraphic units of the Kössen Formation showing facies associations with sample-level abundances of brachiopod genera. Based on our field data. (A) Middle parts of the Hochalm Member with samples dominated by *Rhaetina gregaria*. (B) Uppermost part of the Hochalm Member in three sections showing transition into coral beds with scleractinian *Retiophyllia*. Samples are characterized by common *Zeilleria* and *Rhaetina pyriformis*. (C) Boundary between the Hochalm and Eiberg members showing transition into deep-water facies represented by alternation of marlstones and micritic limestones. Rhynchonellids and *Zugmayerella* are common here.

Hettangian deposits. The Hettangian deposits are represented by two formations (Fig. 4). The Kendlbach Formation consists of deposits originating in the former Kössen Basin. The Schnöll Formation is formed by deposits originating at places of the former patch-reef production. The upper boundary of the Kendlbach and Schnöll formations is marked by Fe-Mn crusts or by the Enzesfeld Limestone (Upper Hettangian – lowermost Sinemurian). The Kendlbach Formation starts with the boundary marl at the base, followed by the siliciclastic-rich Tiefengraben Member and terminated by the carbonate-rich Breitenberg Member (Fig. 4; Golebiowski and Braunstein, 1988). A several meters thick boundary marl has low carbonate content and contains layers which can be enriched with bitumen, pyrite, quartz and mica admixture (Golebiowski and Braunstein, 1988). In the western part of the NCA, the lower parts of the boundary marl are represented by red marlstones and siltstones (Schattwald Shale). Although there are no ammonites, the boundary marl contains rare lingulids, Hettangian bivalves and palynomorphs. The only known rhynchonelliformean brachiopods are rhynchonellids from the Karwendelmunde section (Axel von Hillebrandt, pers. comm., 2005). The Tiefengraben Member is characterized by a relatively uniform alternation of micritic limestones and marlstones with rare bivalves (Fig. 4). The first occurrence datum of *Psiloceras calliphyllum* is in the Breitenberg member. This member is formed by microintraclastic-bioclastic packstones and grainstones with bivalves and brachiopods of the Early Hettangian age. In some sections, the boundary between the Tiefengraben and Breitenberg Member is more gradual, represented by alternation of marls and bioclastic limestones (Fig. 4). The deposits of the Middle Hettangian *Kammerkarites megastoma* Zone are thin or missing in the Breitenberg Member (Kment, 2000).

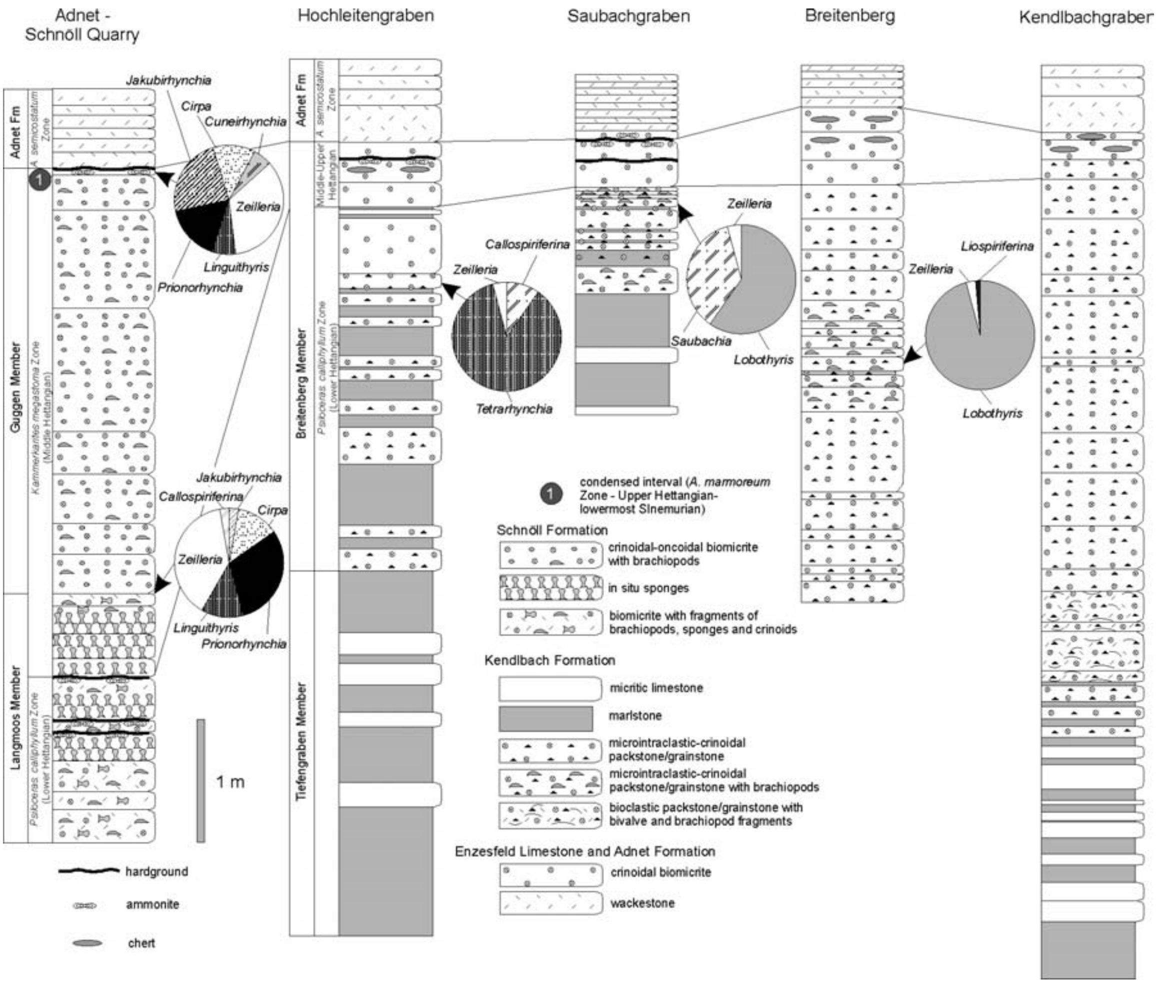


Figure 4 – Facies associations of the Hettangian deposits in the area of Osterhorngruppe (SE of Salzburg) shown in four sections with the Kendlbach Formation, and one section with the Schnöll Formation. Sample-level abundances of brachiopod genera illustrate compositional differences between formations and between stratigraphic zones. Based on our field data. The correlation is based on biostratigraphic data in Suess and Mojsisovics (1868), Blind (1963), Plöchinger (1975), Blau and Grün (1996) and Böhm et al. (1999). The *P. calliphyllum* Zone is restricted to the Breitenberg Member.

In the areas of Triassic coral reefs, the time interval represented by the deposition of the boundary marl and Tiefengraben Member is mostly represented by a hiatus. The Lower-Middle Hettangian deposits are represented by cross-bedded limestones of the Breitenberg Member and by the Schnöll Formation (Böhm et al., 1999; Böhm, 2003). The Schnöll Formation starts with the Langmoos

Member, which is formed by bioclastic wackestones/floatstones with common in situ silicisponges (Delecat and Reitner, 2005), stromatactites, crinoids and brachiopods (Fig. 4). The Langmoos Member passes upward into the Guggen Member, which is represented by crinoidal-oncoidal wackestones (Fig. 4). The Breitenberg or Guggen members pass upward into red nodular limestones of the Adnet Formation (Fig. 4). At their boundary, the Enzesfeld Limestone formed by biomicritic wackestones, packstones and Fe-Mn crusts contains brachiopods of the *Angulaticeras marmoreum* Zone (Böhm et al., 1999; Kment, 2000).

Methods

Two datasets based on new field data and literature compilations are analysed. The first one consists of 62 samples and 2861 brachiopod specimens from the Kössen Formation, patch-reefs ("Oberrhät" Limestone) and the Starhemberg Limestone of Rhaetian age (Golebiowski, 1989; Siblík, 1998; Turnšek et al., 1999; and 25 unpublished samples). The second dataset is formed by 15 samples and 975 brachiopod specimens from the Hettangian Kendlbach and Schnöll Formation, and the Enzesfeld Limestone (Siblík, 1993a, b, 1999; Böhm et al., 1999; and 4 unpublished samples). The samples correspond either to one bed or to a group of beds of similar lithology. With the exception of the Enzesfeld Limestone which can be biostratigraphically condensed, they represent census or within-habitat time-averaged relicts of local communities. The samples come from the central and eastern part of the NCA. The westernmost part of the NCA (e.g., Vorarlberg, McRoberts et al., 1997), the Restental Member and the Zlambach Formation are not represented in our datasets. However, species and generic composition of the communities of the Kössen Basin is representative of the northern Tethyan margin.

Due to taxonomic inconsistencies, all analyses are performed on generic level with two exceptions. (1) *Rhaetina gregaria* and *Rhaetina pyriformis* are treated separately during exploratory multivariate analyses due to their different stratigraphic and environmental distribution. However, they are pooled into one genus when differences between habitats and between time intervals are tested. (2) Due to taxonomic inconsistencies, absolute abundances of Rhaetian rhynchonellids *Fissirhynchia fissicostata* (Suess, 1854), ?*Calcirhynchia subrimosa* (Schafhäutl, 1851) and rhynchonellid sp. A (corresponding to *“Rhynchonella” subrimosa* of Suess, 1854) are pooled into “rhynchonellids”. Although the generic assignments of ?*C. subrimosa* and rhynchonellid sp. A are not resolved, it is probable that they represent genera other than *Fissirhynchia*. These three rhynchonellids are assigned to the family Cyclothyrididae and superfamily Hemithiridoidea because they possess the canalifer crura. Taxonomic classification above the generic level follows Carter et al. (1994) and Savage et al. (2002).

Abundance genus-level data are summarized in the Supplement. Genera that are represented in the whole dataset by one or two specimens only were omitted (including *Bactrynium, Thecospira, Securithyris*, *Bakonyithyris*, *Securina, “Rhynchonella”* aff. *paolii* and *“Terebratula” juvavica*). The generic assignments follow the published determinations with an exception of one revised rhynchonellid genus (Tomašových, 2006a). Absolute numbers of brachiopod specimens were converted to relative abundances. Three types of multivariate methods are used, including cluster analysis based on Bray-Curtis similarity and group average clustering method, non-metric multidimensional scaling (NMDS) and detrended correspondence analysis (DCA). NMDS is explicitly based on rank-order, Bray-Curtis dissimilarity matrix and makes no assumptions about the shape of species response to an environmental gradient. In Q-mode NMDS analyses, if Bray-Curtis similarity is 100, two samples have identical composition. If it is 0, two samples have no species in common. In R-mode NMDS analyses, if Bray-Curtis similarity is 100, abundances of two genera are the same in all samples; if it is 0, two genera have no samples in common. NMDS is used here for visualizing of between-sample differences in taxonomic composition (De`ath, 1999). In this study, NMDS with three pre-specified dimensions was repeated twenty times with different random positions of samples or taxa in starting configurations. DCA is implicitly based on Chi-square distance matrix and assumes the unimodal response of species distributions along an environmental gradient. Detrending procedure creates artefactual diamond- or triangle-shaped patterns (Kenkel and Orlóci, 1986; Minchin, 1987). However, sample scores along the first axis might be highly correlated with environmental gradients (Holland et al., 2001; Scarponi and Kowalewski, 2004; Holland, 2005). Sample scores along the first DCA axis will be used here as an approximate measure of beta diversity. The first DCA axis is re-scaled in standard deviation (SD) units. A 50% change in sample composition is approximately recorded as 1-1.4 SD units and a complete turnover correspond to about four SD units (Hill and Gauch, 1980).

One-factorial analysis of similarities (ANOSIM) is used for testing whether average rank dissimilarity within habitats or stratigraphic zones, based on Bray-Curtis coefficient, is significantly lower than average rank dissimilarity between habitats or stratigraphic zones (Clarke and Green, 1988). If the null hypothesis (e.g., there are no differences in composition among habitats or among zones) is rejected, the pattern that average rank dissimilarities within habitats are smaller than those between habitats cannot be produced by a chance. Test statistic (R) attains the values from -1 to 1. It is approximately zero if the null hypothesis is true, so average of rank dissimilarities between and within habitats will be more or less the same. Large values close to one are indicative of complete compositional separation of habitats or zones. Significance levels are computed with a general randomization Monte Carlo approach. All analyses were done with the PRIMER software (Clarke and Warwick, 2001), with the exception of DCA (PAST software, Hammer et al., 2001).

Based on a geological time scale of Gradstein et al. (2004), the Rhaetian age has duration of about 4 Ma and the Hettangian age of about 3 Ma. Therefore, the Rhaetian and Hettangian zones can have approximately comparable duration (i.e., ca. 1 Ma). The stratigraphic units of the Kössen Formation defined by Golebiowski unit are also used in some analyses. Three habitats are distinguished, including (1) habitats above normal storm wave base (NSWB) with signs of frequent storm disturbance (i.e., amalgamation of storm-reworked beds and signs of sorting and wave or current preferred orientation), (2) below NSWB with signs of rare storm disturbance (i.e., thin layers of storm-reworked bed embedded between marlstones or micrite-rich limestones), and (3) below maximum storm wave base (MSWB) with missing signs of storm disturbance. The habitats above fair-weather wave base (FWWB) are not represented in our dataset. The habitats were either directly scored in the field or the habitat assignments were based on published sections (Golebiowski, 1989; Böhm et al., 1999).

Analyses of Rhaetian and Hettangian datasets are divided in two parts. First, the communities are discriminated with cluster analyses, relationship between samples and genera is evaluated with NMDS, and beta diversity is assessed in DCA. Second, ANOSIM is used for testing whether there is any significant difference in composition among stratigraphic zones and among habitats. The first hypothesis testing the differences in composition between Rhaetian and Hettangian communities is evaluated with ANOSIM by comparing (1) the Rhaetian and Hettangian stage, and (2) the Rhaetian and Hettangian zones on genus, family, superfamily, suborder, and order levels. The second hypothesis tests the differences in environmental distribution of suborders and orders with time-environment diagrams (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985).

Rhaetian

Rhaetian brachiopod communities. Q-mode cluster analysis of 62 samples discriminated five sample groups at Bray-Curtis similarity corresponding to 40 (Fig. 5A). They are termed as communities in this paper (paleocommunity types in terms of Bambach and Bennington, 1996). At Bray-Curtis similarity of 50, the Rhynchonellid community can be further subdivided into three subcommunities and the *Oxycolpella* community into two subcommunities. This subdivision into subcommunities is adopted here because the pooling of samples into the communities obscures their sample-level relative abundances (Fig. 6). Q-mode NMDS (Fig. 5B) and DCA (Fig. 5C) indicate that with the exception of the *R. gregaria* community, the communities show gradual transitions in terms of their composition. The *R. pyriformis* community is compositionally replaced by the *Zugmayerella*, Rhynchonellid and *Oxycolpella* communities. The maximum sample score is 2.8 along the first axis, implying the gradient length of 2.8 SD units and relatively moderate beta diversity. However, the *R. gregaria* and the *Oxycolpella* communities do not share any species in common, indicating almost complete turnover along the gradient.

(1) The *Rhaetina gregaria* community is represented by nine samples with 315 specimens. *R. gregaria* commonly occurs in shell concentrations, associated with less common bivalves (*Atreta, Rhaetavicula, Gervillaria, Chlamys, Liostrea*). This community occurs in the *Sagenites reticulatus* Zone only. It occurs either in coral debris or bioclastic floatstones in the carbonate intervals or in marly floatstones in the lower parts of the siliciclastic intervals (Fig. 3A).

(2) The *Zugmayerella* community is represented by three samples with 193 specimens. *Zugmayerella* (mainly *Z. koessenensis*, 70%) dominates, followed by less common *Zeilleria* (24%) and rare *Austrirhynchia* (5%). Rhynchonellids, *Oxycolpella* and *R. pyriformis* are very rare (below 1%). Epifaunal bivalves (*Chlamys* and *Plagiostoma*) are common. The community is limited to coral-bioclastic limestones or bioclastic marlstones near patch-reefs in the *Vandaites sturzenbaumi* Zone.

(3) The *Rhaetina pyriformis* community is represented by 15 samples and 351 specimens. *R. pyriformis* is dominant (54%); *Zeilleria* (19%), *Zugmayerella* (12%), *Austrirhynchia* (8%) and *R. gregaria* (6%) are less common. From bivalves, *Chlamys, Plagiostoma, Gervillaria, Atreta* and *Actinostreon* are present. It occurs in coral debris floatstones and coral framestones of the *V. sturzenbaumi* Zone (Fig. 3B).

(4) The Rhynchonellid community consists of three subcommunities. The *Zeilleria-Rhaetina pyriformis* subcommunity represented by six samples with 351 specimens occurs in bioclastic marlstones and coral beds of the *V. sturzenbaumi* Zone. *Zeilleria* (26%) and *R. pyriformis* (24%) are abundant; rhynchonellids (19%), *Zugmayerella* (11%), *R. gregaria* (9%) and *Austrirhynchia* (8%) are less common. *Triadithyris* is rare (2%). Bivalves are mainly represented by *Gervillaria* and *Actinostreon*. The Rhynchonellid-*Zeilleria* subcommunity is represented by eight samples with 254 specimens and occurs in coral debris floatstones and marly limestones and marlstones of the *V. sturzenbaumi* and *Choristoceras marshi* zones. Rhynchonellids dominate (46%); *Zeilleria* (21%), *Zugmayerella* (15%) and *R. pyriformis* (9%) are less common. *Austrirhynchia* (5%) and *Oxycolpella* (1%) are rare. Bivalves *Atreta, Plagiostoma* and *Oxytoma* can occur in this subcommunity. The

Rhynchonellid subcommunity is represented by eight samples with 721 specimens. It occurs in biomicritic limestones and marlstones in the *V. sturzenbaumi* and *C. marshi* zones. Rhynchonellids strongly dominate (85%). *Austrirhynchia* (6%), *Zeilleria* (3%), *Oxycolpella* (3%), *Zugmayerella* (2%) and *Sinucosta* (1%) are rare. Bivalves *Chlamys, Oxytoma* and *Atreta* typically occur in this subcommunity.

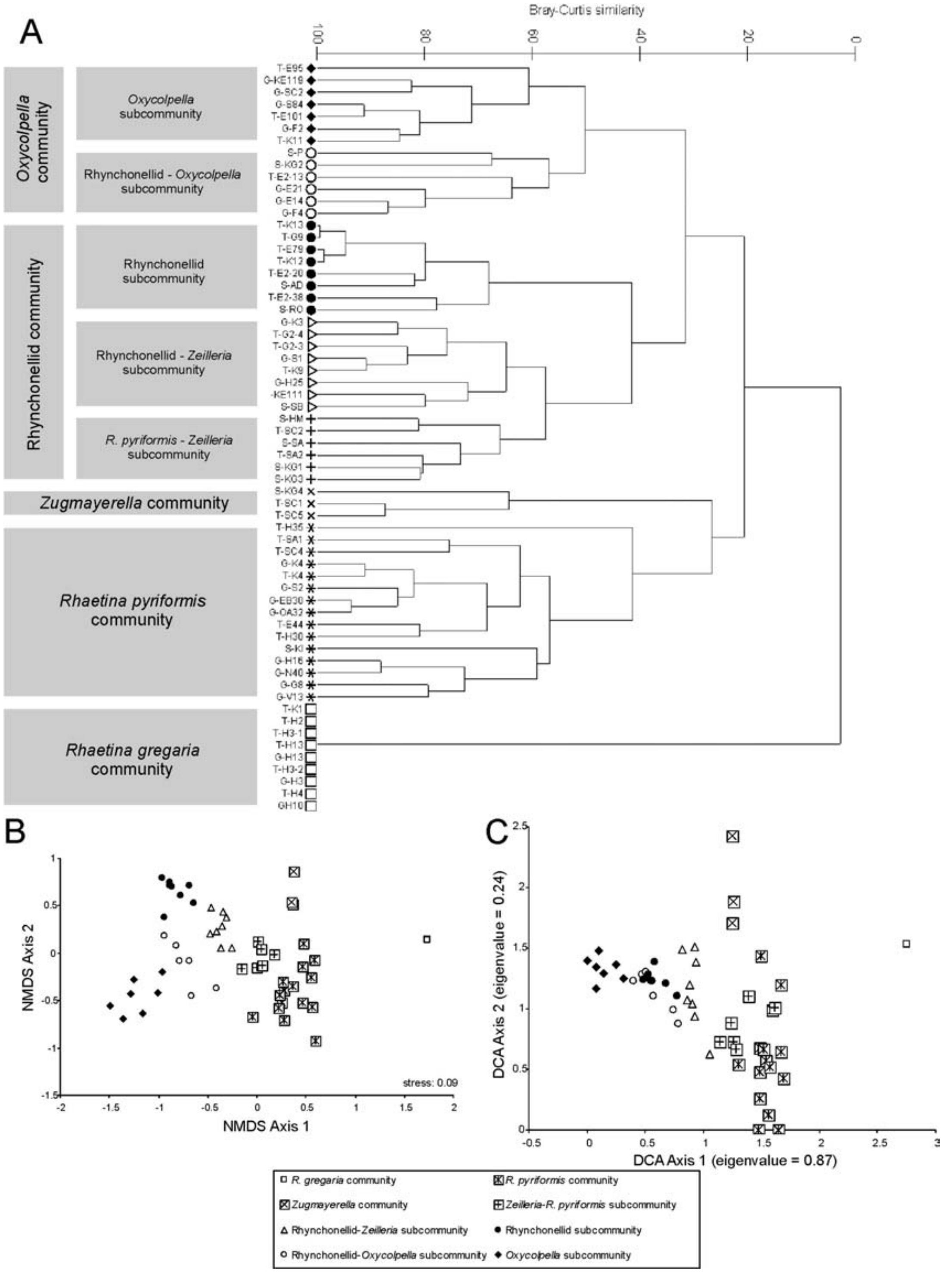


Figure 5 - Rhaetian communities. (A) Q-mode cluster analysis. (B) Q-mode non-metric multidimensional scaling (NMDS). Note that the scaling and orientation of axes in NMDS are arbitrary. The configuration is rotated to have the greatest variation along the first axis for visual convenience. (C) Detrended correspondence analysis of samples (genera are shown in Figure 7). Note that nine samples of the *Rhaetina gregaria* community correspond to one point in NDMS and DCA plots.

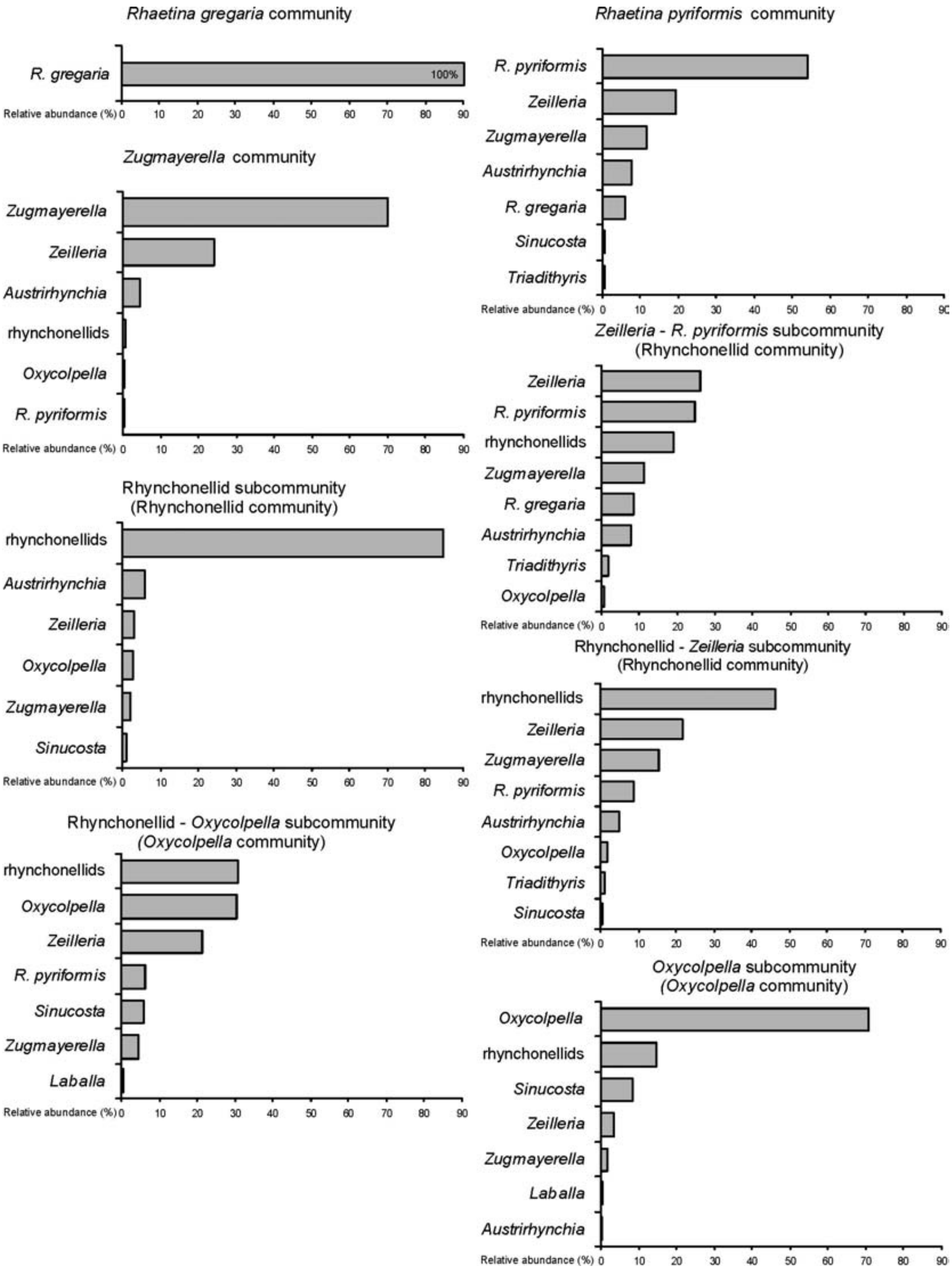


Figure 6 - Relative abundances of brachiopods in five Rhaetian communities with five subcommunities.

(5) The *Oxycolpella* community consists of two subcommunities. The Rhynchonellid-*Oxycolpella* subcommunity is represented by six samples with 407 specimens and occurs mainly in biomicritic limestones and marlstones of the *V. sturzenbaumi* and *C. marshi* zones. Rhynchonellids and *Oxycolpella* are equally abundant (30%); *Zeilleria* (22%) is less common. *R. pyriformis* (6%), *Sinucosta* (6%) and *Zugmayerella* (5%) are rare. Bivalves (*Chlamys*) are very rare. The *Oxycolpella* subcommunity consists of seven samples formed by 269 specimens and is limited to biomicritic limestones and marlstones of the *C. marshi* Zone. *Oxycolpella* is dominant (71%); rhynchonellids

(15%) and *Sinucosta* (9%) are less common. Other brachiopods as *Zeilleria* (3%) and *Zugmayerella* (2%) are rare. Bivalves (*Chlamys, Oxytoma* and *Cassianella*) are rare.

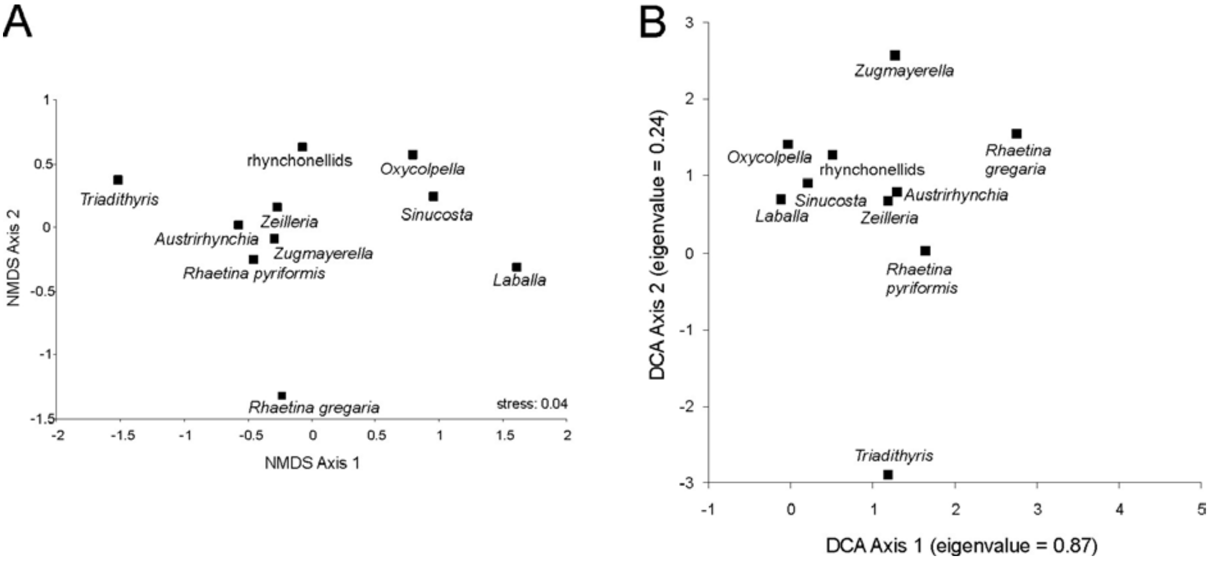


Figure 7 - Abundance patterns of Rhaetian brachiopods. (A) R-mode non-metric multidimensional scaling (NMDS). The configuration is rotated to have the greatest variation along the first axis for visual convenience. (B) Detrended correspondence analysis of genera and two species of *Rhaetina.*

Co-existence patterns of Rhaetian brachiopod genera. In R-mode NMDS, *R. gregaria* is distinctively separated from all other genera and has the highest Bray-Curtis similarity with to *R. pyriformis*. *R. pyriformis* have higher Bray-Curtis similarities with *Zugmayerella* and *Zeilleria* than with rhynchonellids (Fig. 7A). Finally, *Oxycolpella, Sinucosta* and rhynchonellids form the group of closely co-existing taxa with similar abundance patterns. *R. gregaria* is strongly segregated from other brachiopods in DCA (Fig. 7B). The ordination of genera along the first axis in DCA is comparable to the compositional replacement in R-mode NMDS (i.e., *R. pyriformis* is replaced by *Zugmayerella*, *Zeilleria*, rhynchonellids and *Oxycolpella*).

Linking Rhaetian brachiopods to stratigraphy. The global ANOSIM and pairwise comparisons among three zones demonstrate significant differences in community composition ($R = 0.57$, $p < 0.0001$, Table 1). The difference between the *S. reticulatus* and *V. sturzenbaumi* zones corresponds to the replacement of the *R. gregaria* community by the *R. pyriformis*, *Zugmayerella* and Rhynchonellid communities (Fig. 8). The difference between the *V. sturzenbaumi* and *C. marshi* zones corresponds to the disappearance of the *R. pyriformis* and *Zugmayerella* communities and the appearance of the *Oxycolpella* community in the *C. marshi* Zone (Fig. 8). This test indicates a substantial taxonomic turnover among stratigraphic zones within the Kössen Basin. The communities dominated by *Zugmayerella* in the Hochalm Member are missing in the middle and upper parts of the Eiberg Member in the Kössen Basin. However, they occur in siliciclastic-rich, shallow habitats of the *C. marshi* Zone in the Frankenfels Nappe (Bajuvaric Unit, Golebiowski, 1991). In addition, the *R. gregaria* and *R. pyriformis* communities persist to the Late Rhaetian in the West Carpathians (Michalík, 1973a; Michalík et al., 1979).

Stratigraphic zones	R Statistic	P-value	Permutations	Number of permuted R≥observed R
Rhaetian - global test	0.57	<0.0001	10000	0
Rhaetian - pairwise tests:				
S. reticulatus Zone vs. *V. sturzenbaumi* Zone	0.278	0.004	10000	35
V. sturzenbaumi Zone vs. *C. marshi* Zone	0.568	<0.0001	10000	0
S. reticulatus Zone vs. *C. marshi* Zone	0.986	<0.0001	10000	0
Hettangian - global test	0.421	0.007	10000	69
Hettangian - pairwise tests:				
P. calliphyllum Zone vs. *K. megastoma* Zone	0.534	0.007	1287	9
A. marmoreum Zone vs. *K. megastoma* Zone	0.282	(0.24)	21	5
P. calliphyllum Zone vs. *A. marmoreum* Zone	0.308	(0.11)	45	5

Table 1 - Results of ANOSIM showing differences in composition among Rhaetian zones and among Hettangian zones. Pairwise comparisons between the Unit 2 and all other units are not shown as they are always significant at p<0.0001 (R is mostly close to one). For pairwise comparisons, the alpha value is 0.016 (0.05/3) using the Bonferroni correction. The p-values in parentheses are inconclusive due to low number of permutations.

Linking Rhaetian brachiopods to environment. The differences in community composition among three habitats are significant with global ANOSIM ($R = 0.396$, $p < 0.0001$). Pairwise comparisons show that the difference between habitats below and above MSWB is significant only (Table 2). Due to the high compositional turnover among stratigraphic zones, testing among habitats is restricted within four stratigraphic levels (Table 2).

(1) Monospecific assemblages with *R. gregaria* in Unit 2 of the Hochalm Member occupied habitats above NSWB and below NSWB. They occur in coral patch-reefs, shell-rich floatstones and packstones, micrite-rich floatstones and marly mudstones.

(2) Habitats above and below NSWB in units 3 and 4 of the Hochalm Member are significantly different in community composition ($R = 0.258$, $p = 0.007$). Habitats below NSWB associated with coral beds or bioclast-rich bottom were inhabited by the *R. pyriformis* or the *Zugmayerella* community (Fig. 9A). Habitats above NSWB associated with coral patch-reefs were inhabited by the *R. pyriformis* community, and the *Zeilleria-R. pyriformis* and Rhynchonellid-*Zeilleria* subcommunities. They were occupied by more common rhynchonellids in contrast to the habitats below NSWB (Fig. 9A). Note that siliciclastic, soft-bottom habitats below MSWB are represented by marlstones that contain rare brachiopods.

(3) The difference between habitats above and below MSWB in units 5-7 of the Eiberg Member is of borderline significance ($R = 0.3$, $p = 0.042$). Habitats below NSWB with bioclastic micritic substrate were occupied mainly by the *Zugmayerella* and Rhynchonellid communities (Fig. 9B). Habitats below MSWB with marly micritic substrate were inhabited by the Rhynchonellid and *Oxycolpella* communities. Habitats above NSWB are not represented in our dataset.

(4) Habitats above and below MSWB in Unit 8 of the Eiberg Member show also differences in community composition ($R = 0.593$). Patch-reefs above MSWB (habitats above and below NSWB are not differentiated in this case) were inhabited by the Rhynchonellid and Rhynchonellid-*Oxycolpella* subcommunities (Fig. 9C). Marly micritic habitats below MSWB were dominated by *Oxycolpella*.

The depth- and substrate-related distribution patterns demonstrate that the particular habitats were differentially inhabited by brachiopods at each stratigraphic level (Fig. 9). The habitats between NSWB and MSWB were inhabited by the *R. gregaria* community in Unit 2, by the *R. pyriformis* community in units 3-4, by the *Zugmayerella* community in units 5-7 and by the Rhynchonellid community in Unit 8. Habitats below MSWB were dominated by the Rhynchonellid community in units 5-7 and by the *Oxycolpella* community in Unit 8. On one hand, some genera preferred particular habitats along the bathymetric transect. *Zugmayerella* was most abundant in habitats between NSWB and MSWB, *Rhaetina* was most common above MSWB and *Oxycolpella* was most common below MSWB. On the other hand, *Zeilleria* was a generalist in terms of substrate and depth distribution because it occurred across the whole onshore-offshore transect. Rhynchonellids were also generalists in terms of their depth distribution. They were more common in shallow than in deep habitats in units 3-4 and in Unit 8; in contrast, they were more common in deep habitats in units 5-7.

Rhaetian - all samples	R Statistic	P-value (*<0.016)	Actual Permutations	Number of permuted R≥observed R
Global test	0.396	<0.0001	10000	0
Pairwise tests:				
Above NSWB vs. below NSWB	0.019	0.21	10000	2191
Below NSWB vs. below MSWB	0.71	<0.0001	10000	0
Above NSWB vs. below MSWB	0.41	<0.0001	10000	0
Rhaetian - stratigraphic levels				
Hochalm Member (units 3-4)				
Above NSWB vs. below NSWB	0.258	0.007	10000	70
Eiberg Member (units 5-7)				
Below NSWB vs. below MSWB	0.306	0.042	10000	252
Eiberg Member (unit 8)				
Below NSWB* vs. below MSWB	0.593	(0.029)	35	1
Hettangian - all samples				
Global test	0.887	<0.0001	10000	0
Pairwise tests:				
Above NSWB vs. below NSWB	0.527	(0.095)	21	2
Below NSWB vs. below MSWB	0.946	(0.022)	45	1
Above NSWB vs. below MSWB	0.978	0.001	1287	1

Table 2 - Results of ANOSIM showing differences among Rhaetian habitats and among Hettangian habitats. For pairwise comparisons, the alpha value is 0.016 (0.05/3) using the Bonferroni correction. The p-values in parentheses are inconclusive due to low number of permutations.

Discussion. Although the compositional differences among stratigraphic zones are significant, they are biased by spatial coverage of the analysed samples and do not represent large-scale turnover caused by extinctions of dominant taxa during the Early Rhaetian. All communities and their dominant taxa persisted in the Western Tethys up to the upper parts of the *C. marshi* Zone, indicating that their compositional variation and between-habitat differentiation were relatively stable during the Rhaetian. Brachiopods migrated or tracked their habitats into areas more proximal to the shoreline during this time interval. The disappearance of the *R. gregaria*, *R. pyriformis* and *Zugmayerella* communities during the Late Rhaetian was a local feature of the Kössen Basin.

With the exception of the *R. gregaria* community, the compositional overlaps indicate that the communities were not discrete and were composed of taxa with broadly overlapping habitat preferences. The effects of depth and substrate on environmental separation of brachiopods are demonstrated by between-habitat differences in community composition at each stratigraphic level. For example, effects of substrate can reflect the differences between coral beds and coral patch-reefs in the Hochalm Member, or the differences between micritic and coral substrates in the Eiberg Member.

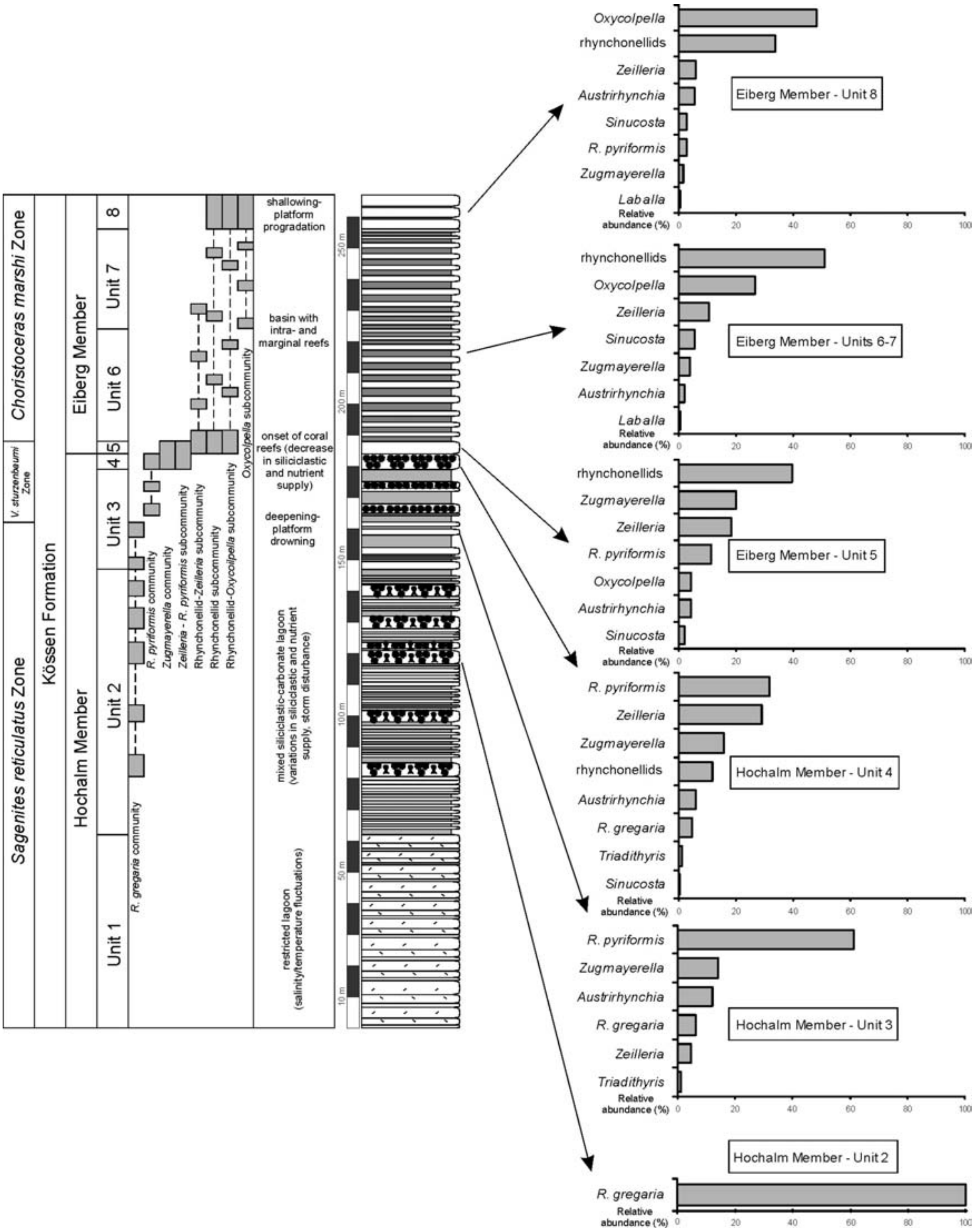


Figure 8 - Stratigraphic distribution of Rhaetian communities and pooled compositions of eight stratigraphic units of the Kössen Formation. Note that the changes in environmental history of the Kössen Basin correlate with the community replacement. Explanations as in Fig. 2.

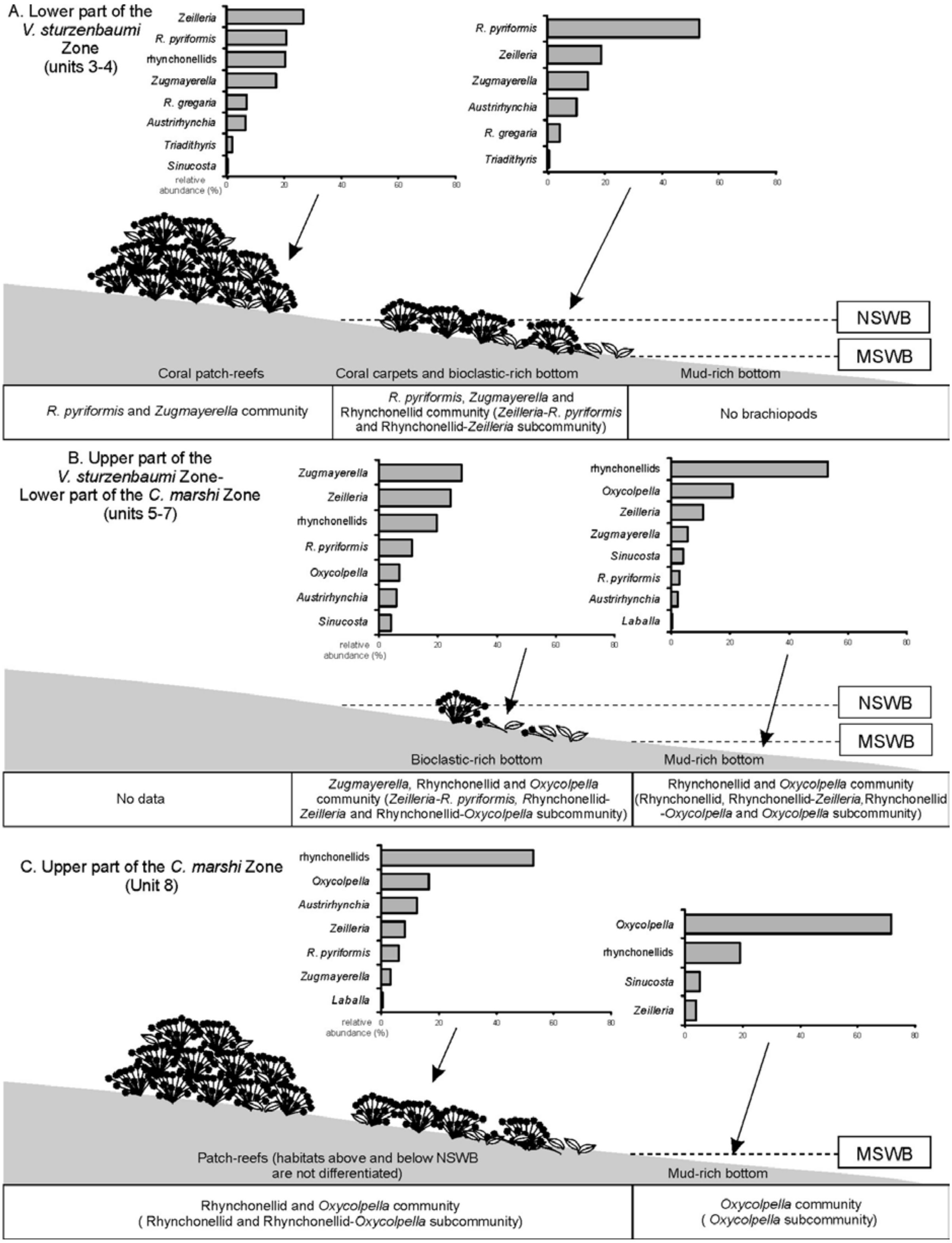


Figure 9 - Compositional variation of Rhaetian communities along depth gradients. Note that habitats were occupied by different communities at each stratigraphic level. (A) Hochalm Member – units 3 and 4. (B) Eiberg Member – units 5-7. (C) Eiberg Member – Unit 8.

The overlap in the depth distribution between *R. gregaria* and *R. pyriformis* is in contrast to their supposed depth differentiation as suggested by Golebiowski (1991). However, although *R. gregaria* and *R. pyriformis* both occupy habitats above MSWB, their replacement coincides with the decrease in the frequency and thickness of storm-reworked beds, indicating a net increase in relative sea level (Golebiowski, 1990). In the Fatric Unit of the West Carpathians, *R. gregaria* inhabited habitats above MSWB. This species persisted up to uppermost parts of the Rhaetian deposits in habitats which were very proximal to the shoreline (Michalík et al., 1979; Michalík, 1982; Tomašových, 2004b). In contrast, *R. pyriformis* occurred in the West Carpathian habitats that were more distal to the shoreline (Hronic Unit, Michalík, 1973a). Based on growth line patterns, Tomašových and Farkaš (2005) demonstrated that *R. gregaria* lived in habitats with relatively higher environmental instability (e.g., higher seasonality leading to variations in temperature, nutrient supply or turbidity) in contrast to *R. pyriformis*. The lower environmental variation caused by reduced proximity to shoreline and better connection with open sea can thus explain the replacement of *R. gregaria* by *R. pyriformis* in the higher part of the Hochalm Member.

The appearance of the *Zugmayerella* community and the *Zeilleria-R. pyriformis* subcommunity in the Kössen Basin correlated with the onset of widespread colonization of the Kössen Basin by corals. Both communities were consistently associated with coral habitats above MSWB This increase in compositional variation (i.e., several communities in Unit 4 in contrast to *R. pyriformis* in Unit 3) could reflect an increase in heterogeneity in coral reefs habitats and a decrease in siliciclastic supply and turbidity (as compared to thin coral carpets between siliciclastic beds in Unit 3).

With the onset of basin deposition of the Eiberg Member, the Rhynchonellid and *Oxycolpella* communities inhabited soft-bottom habitats below MSWB. The compositional change between the Hochalm and Eiberg Member might be related to a change in sediment supply and substrate stability. In the siliciclastic-rich intervals, palynofacies and trace elements indicate nutrient-rich conditions coupled with low oxygen levels (Holstein, 2004). New increase in sea level might lead to new immigration episodes (e.g., *Oxycolpella* appears in Unit 5 for the first time). Finally, deposits of Unit 8 indicate new shallowing and perhaps restriction of the Kössen Basin (e.g., progradation of the “Oberrhät” Limestone over the Eiberg Member at Steinplatte, Stanton and Flügel, 1989, 1995; Bernecker et al., 1999). The community replacement in the Kössen Basin thus reflects combined effects of habitat tracking and immigration/local extinction events, possibly related to climatic and sea level changes (e.g., Aberhan, 1993; Brett, 1998; Buzas and Culver, 1998).

Hettangian

Hettangian brachiopod communities. Although the samples from the Kendlbach Formation form one cluster (Fig. 10A), two samples dominated by *Tetrarhynchia* and *Callospiriferina* have a distinct composition in contrast to other five samples dominated by *Lobothyris*. The *Lobothyris* sample group forms one cluster at Bray-Curtis similarity of 50 (Fig. 10A) and its separation from the samples dominated by *Tetrarhynchia* and *Callospiriferina* is also visible in Q-mode NMDS (Figs. 10B-C). Therefore, the samples from Hochleitengraben and Vorderer Ampelsbach are assigned to the *Tetrarhynchia-Callospiriferina* sample group, although each sample is dominated by different genus. The third sample group is typical of the Schnöll Formation and the Enzesfeld Limestone. One sample from the Schnöll Formation is dominated by *Liospiriferina* (Fig. 11). NMDS and DCA show a strong compositional segregation of the first two sample groups from the Kendlbach Formation in comparison to the samples from the Schnöll Formation and Enzesfeld Limestone (Fig. 10B-C). The gradient length along the first DCA axis is five SD units long, indicating a complete turnover and relatively high beta diversity.

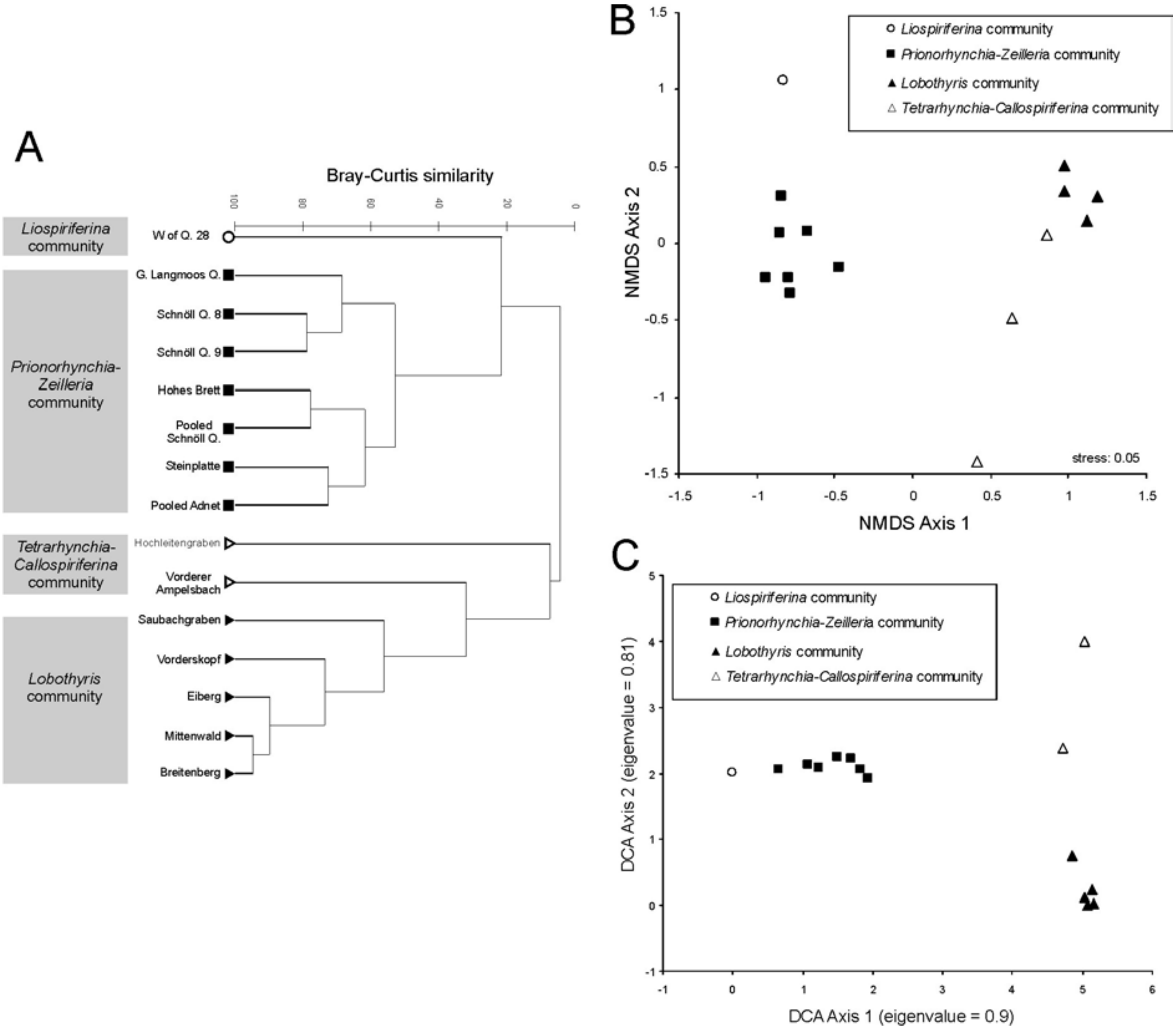


Figure 10 - Hettangian communities. (A) Q-mode cluster analysis. (B) Q-mode non-metric multidimensional scaling (NMDS). The configuration is rotated to have the greatest variation along the first axis for visual convenience. (C) Detrended correspondence analysis of samples (genera are shown in Figure 12).

1) The *Lobothyris* community is represented by five samples with 368 specimens. *Lobothyris* dominates (81%), rhynchonellid *Saubachia* (8%) and spiriferinid *Callospiriferina* (5%) are less common. Other rhynchonellids (*Piarorhynchia* and *Jakubirhynchia*, 2%) and *Zeilleria* (1%) are rare. Bivalve *Plagiostoma* can be very common. This community consistently occurs in microintraclastic-crinoidal packstones/grainstones in the upper part of the Breitenberg Member (*P. calliphyllum* Zone). Rhynchonellid *Saubachia* is abundant at Saubachgraben where packstones alternate with marlstones (Fig. 4).

(2) The *Tetrarhynchia-Callospiriferina* community is represented by two samples with 216 specimens. Rhynchonellid *Tetrarhynchia* (48%) and spiriferinid *Callospiriferina* (33%) are dominant. *Lobothyris* (13%) and *Zeilleria* (6%) are less common. They occur in marly limestones and marlstones of the Breitenberg Member (*P. calliphyllum* Zone).

(3) The *Prionorhynchia-Zeilleria* community is represented by seven samples with 353 specimens. *Prionorhynchia* (31%) and *Zeilleria* (27%) dominate. *Cirpa* (13%), *Liospiriferina* (11%), *Jakubirhynchia* (8%) and *Linguithyris* (5%) are less common. One sample comes from a dyke infill (*P. calliphyllum* Zone) in the Upper Triassic Dachstein Limestone (Hohes Brett). Four samples are from bioclastic-oncoidal wackestones of the Langmoos Member (*K. megastoma* Zone) and two samples from crinoidal biomicrites of the Enzesfeld Limestone (*A. marmoreum* Zone).

(4) One sample from the Langmoos Member (*K. megastoma* Zone) with 38 specimens is dominated by *Liospiriferina* (82%). *Dispiriferina* (8%) and *Cirpa* (5%) are less common. *Prionorhynchia* (3%) and *Jakubirhynchia* (3%) are rare.

Co-existence patterns of Hettangian brachiopod genera. R-mode NMDS and DCA (Fig. 12) show that the genera typical of the Kendlbach and Schnöll Formation have distinct abundance patterns. A group typical of the Kendlbach Formation is represented by *Lobothyris, Callospiriferina, Tetrarhynchia, Saubachia* and *Piarorhynchia*. A group typical mainly of the Schnöll Formation and Enzesfeld Limestone is represented by *Prionorhynchia, Cirpa, Zeilleria* and *Liospiriferina*. The Bray-Curtis similarities among the genera of the Schnöll Formation and Enzesfeld Formation are higher than similarities among the genera of the Kendlbach Formation.

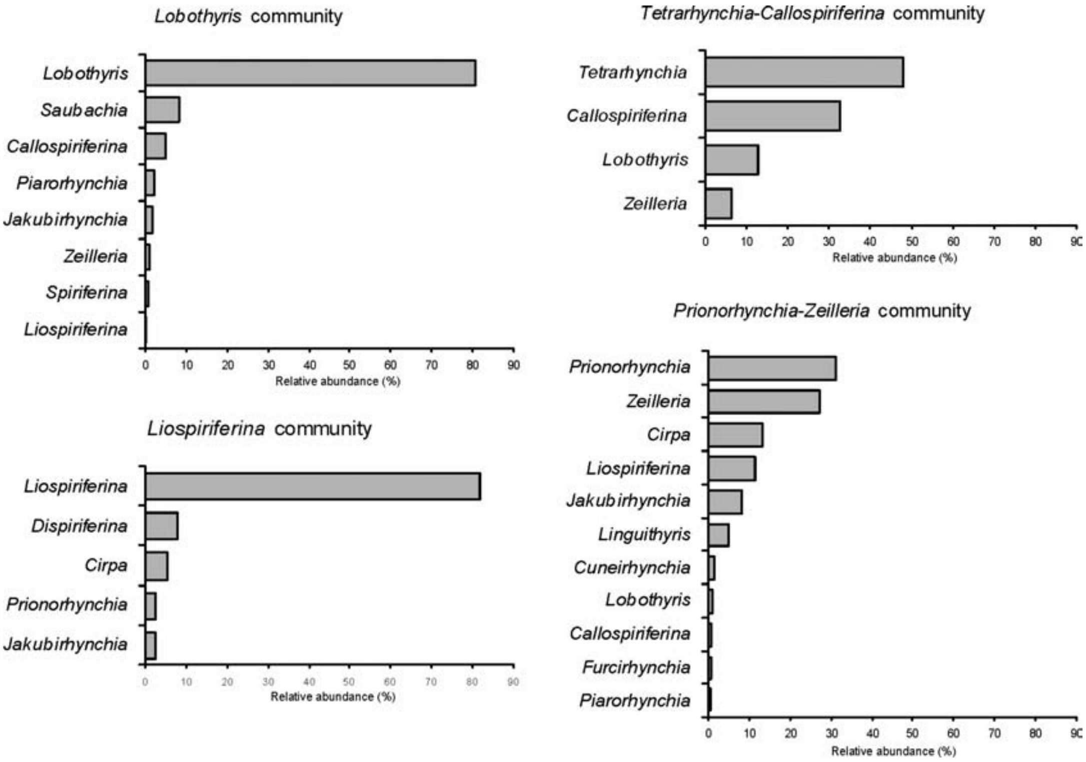


Figure 11 - Relative abundances of brachiopods in four Hettangian communities.

Linking Hettangian brachiopods to stratigraphy. There is a significant difference in community composition between the Lower Hettangian *P. calliphyllum* Zone and the Middle Hettangian *K. megastoma* Zone (R = 0.53, p = 0.007; Table 1). Although the *Prionorhynchia-Zeilleria* community occurs already in the *P. calliphyllum* Zone, the Lower Hettangian deposits are characterized mainly by the *Lobothyris* and *Tetrarhynchia-Callospiriferina* communities typical of the Breitenberg Member. Although *Lobothyris* rarely occurs in the Middle Hettangian deposits of the

Breitenberg Member, this stratigraphic difference indicates that the Early Hettangian communities were rather unique in composition. The Middle and Late Hettangian habitats were occupied mainly by the *Prionorhynchia-Zeilleria* community.

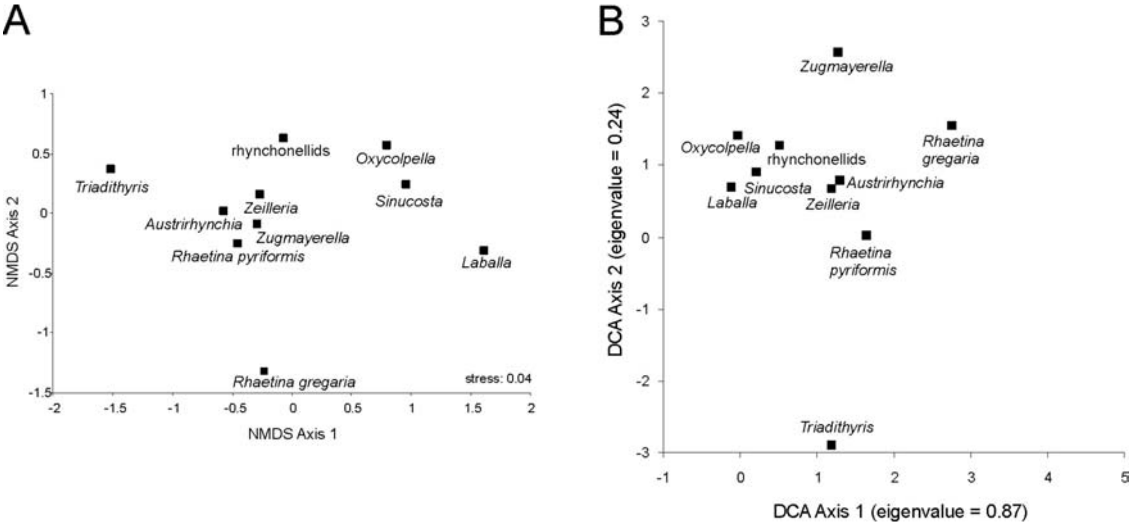


Figure 12 – Abundance patterns of Hettangian brachiopods. (A) R-mode non-metric multidimensional scaling (NMDS). The configuration is rotated to have the greatest variation along the first axis for visual convenience. (B) Detrended correspondence analysis of genera.

Linking Hettangian brachiopods to environment. The samples from three habitats are significantly different in composition (R = 0.89, p = <0.0001; Table 2). Packstones/grainstones and marlstones of the Kendlbach Formation, representing the habitats above and below NSWB, are significantly different in composition from wackestones of the Schnöll Formation, which represent the habitats below MSWB (Table 2). The habitats below NSWB with common marlstone interbeds with abundant rhynchonellids (*Tetrarhynchia* or *Saubachia*) differ in composition from the habitats above NSWB dominated by *Lobothyris* (Fig. 13, R = 0.53; Table 2).

Discussion. Differences in the sediment supply within the Breitenberg Member can be related to the compositional segregation of siliciclastic-rich habitats with abundant rhynchonellids (*Tetrarhynchia* and *Saubachia)*, in contrast to carbonate-rich habitats with high input of microintraclastic and crinoidal debris with abundant *Lobothyris* (Fig. 13). The difference between the communities of the Kendlbach and Schnöll formations correlates with the environmental history of the NCA. Böhm et al. (1999) suggested that carbonate-rich intervals in the upper part of the Kendlbach Formation and approximately coeval sponge layer of the Schnöll Formation were deposited during a sea level rise, leading to reduced siliciclastic supply due to the trapping in shallow habitats and sediment starvation in deep habitats. Environmental separation between communities from the Breitenberg Member on one hand and the Schnöll Formation and Enzesfeld Limestone on the other probably reflects this environmental change (e.g., a change in substrate stability, rate of sedimentation, possibly also in trophic and oceanographic regime). The deposition of the upper part of the Schnöll Formation and Enzesfeld Limestone thus reflects the phase with stable substrate, low turbidity and reduced sedimentation rate. Such conditions favoured the recruitment and colonization by brachiopods of the *Prionorhynchia-Zeilleria* community during the Middle and Late Hettangian.

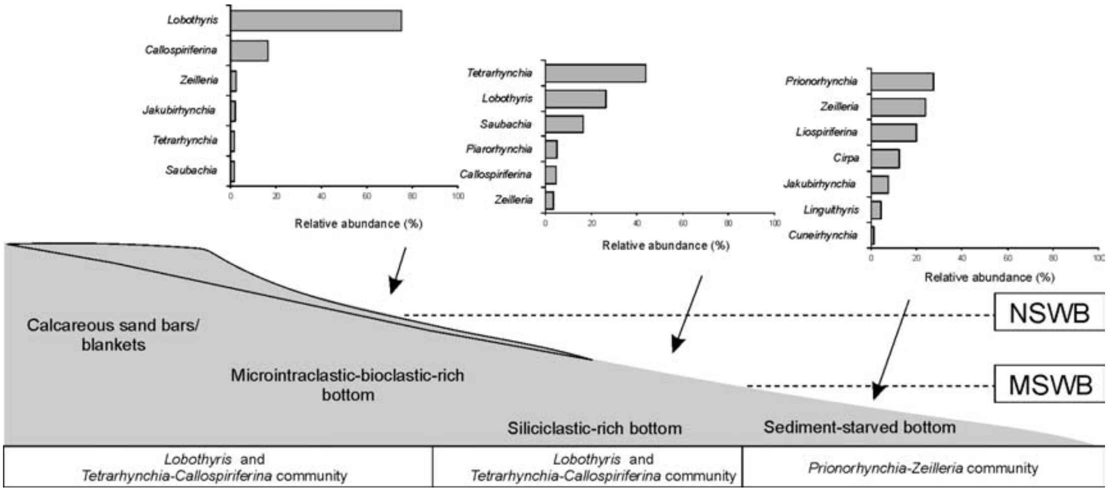


Figure 13 - Compositional variation of Early Hettangian communities along a depth gradient. Carbonate-rich habitats above NSWB were dominated by *Lobothyris*. Rhynchonellids were common in siliciclastic-rich habitats below NSWB. *Prionorhynchia* and *Zeilleria* dominated in deep, sediment-starved habitats.

Recovery of Hettangian brachiopods

Definition. The recovery pattern may be defined in several ways but in general a boundary between a phase characterized by prolonged stress (i.e., extinction/survival phase) and recovery phase is characterized by an increase in origination rates and/or decrease in extinction rates and a return of community-level properties to pre-extinction levels (Erwin, 1998). As taxonomic inconsistencies do not allow evaluating variations in diversity and extinction rates at this stage, compositional variation of brachiopod communities and their environmental distribution are used for evaluation of recovery patterns. Communities in the survival interval are generally supposed to be dominated by ecologic opportunists which occupy physically unstable, disrupted habitats (Schubert and Bottjer, 1995; Kaufmann and Harries, 1996; Harries et al., 1996). During the survival interval, the communities should be dominated by few taxa with broad environmental ranges and between-habitat differentiation of communities should be poor. In contrast, the recovery should be characterized by an increase in number of community types and their between-habitat segregation. Numerically abundant taxa should belong to those which are typical of stable, normal marine conditions later after mass extinction, in contrast to opportunists which are typical of high-stress habitats during "background" times (Harries et al., 1996).

Extinction/survival interval. Rhynchonelliformean brachiopods are very rare in the basal parts of the Kendlbach Formation in the NCA. The only known rhynchonelliformean brachiopods are rhynchonellids from the Karwendelmunde section, which occur in red marls about 1.3 m above the top of the Kössen Formation (Axel von Hillebrandt, pers. comm., 2005). The multicostate rhynchonellids without planareas are 8-11 mm long, posses slightly developed sulcus and fold with 3 or 4 costae. They differ from the rhynchonellids known from the Rhaetian of the western Tethys. They are rather similar to representatives of the family Wellerellidae and Basiliolidae. It is unclear whether they represent surviving opportunists, new immigrants from other regions, or progenitor taxa (i.e., taxa that evolved during the highly stressed intervals during mass extinctions, Kaufman and Harries, 1996). The rarity of brachiopods in the boundary marl is probably a large-scale regional phenomenon because comparable siliciclastic deposits devoid of brachiopods are present also in other areas of the western Tethys (Gaździcki et al., 1979). Highly abundant bivalves in the lower parts of the boundary marl indicate that the taphonomic bias alone does not account for the observed rarity of brachiopods. This implies that the rarity of brachiopods in the lower parts of the boundary marl is a real ecologic signal.

The lower parts of the boundary marl contain abundant shallow infaunal and epifaunal bivalves (Golebiowski and Braunstein, 1988; Rakús and Lobitzer, 1993; McRoberts et al., 1997). *Cardinia* locally forms monospecific, densely-packed concentrations and can be a potential candidate for taxa with high population turnover and opportunistic behaviour that are typical of habitats with high environmental stress (Rodland and Bottjer, 2001). Local signs of lamination, rare bioturbation and bedding planes covered with concordant and complete, disarticulated pteriid and pectinid bivalves imply high environmental stress. The upper clay-rich parts of the boundary marl are mostly completely devoid of shelly benthos.

The lower part of the boundary marl is marked by a negative carbon isotope anomaly, followed by a shift to background levels and a second negative anomaly that characterizes the middle part of the Tiefengraben Member (Krystyn et al., 2005). The return to "background" values approximately correlates with an increasing proportion of bioclastic limestones. This return corresponds with the onset of the Breitenberg Member and the appearance of abundant brachiopods. In addition, palynologic data indicate that an abrupt warming coincides with the initial carbon isotope anomaly. Palynomorph assemblages are characterized by a disappearance of Rhaetian dinoflagellate cysts and a high abundance of prasinophytes (Krystyn et al., 2005). This excursion can hint at an increase in release of methane through dissociation of gas hydrates, an increase in volcanic CO_2 outgassing and/or a decrease in primary productivity (Ward et al., 2001; Pálfy et al., 2001; Hesselbo et al., 2002; Pálfy, 2003; Guex et al., 2004). The second negative carbon-isotope anomaly coincides with a marked turnover in terrestrial palynomorphs (Krystyn et al., 2005). Hautmann (2004a) and Galli et al. (2005) suggested that the increased levels of carbon dioxide could lead to a temporary undersaturation of sea water with respect to calcium carbonate and thus to biocalcification crisis. The combined sedimentologic, geochemical and paleobiologic evidence thus indicates that high-stress conditions were initiated at the base of the boundary marl and continued up to the upper parts of the Tiefengraben Member.

Recovery interval. Three arguments suggest that upper Lower and Middle Hettangian deposits in the NCA correspond to the recovery interval (Fig. 14). First, between-habitat (beta) diversity was even higher during the Middle Hettangian than during the Rhaetian. The Hettangian is represented by lower sample number than the Rhaetian so sampling effects do not account for this difference. In any case, it means that beta diversity of the Middle Hettangian communities was comparable to pre-extinction levels. Second, the between-habitat differentiation of Hettangian brachiopod communities with respect to depth and substrate was comparable to between-habitat differentiation of Rhaetian brachiopod communities. Calcareous sand habitats above NSWB, siliciclastic-rich habitats below NSWB, and carbonate-starved habitats below MSWB were dominated by different brachiopods, implying their distinct environmental preferences. Compositionally, comparable communities occurred also in other regions of the western Tethys during the Hettangian, indicating that the recovery pattern is not restricted to the NCA only. Third, the brachiopods dominating in the Hettangian communities were also typical of normal marine habitats during the Sinemurian and Pliensbachian.

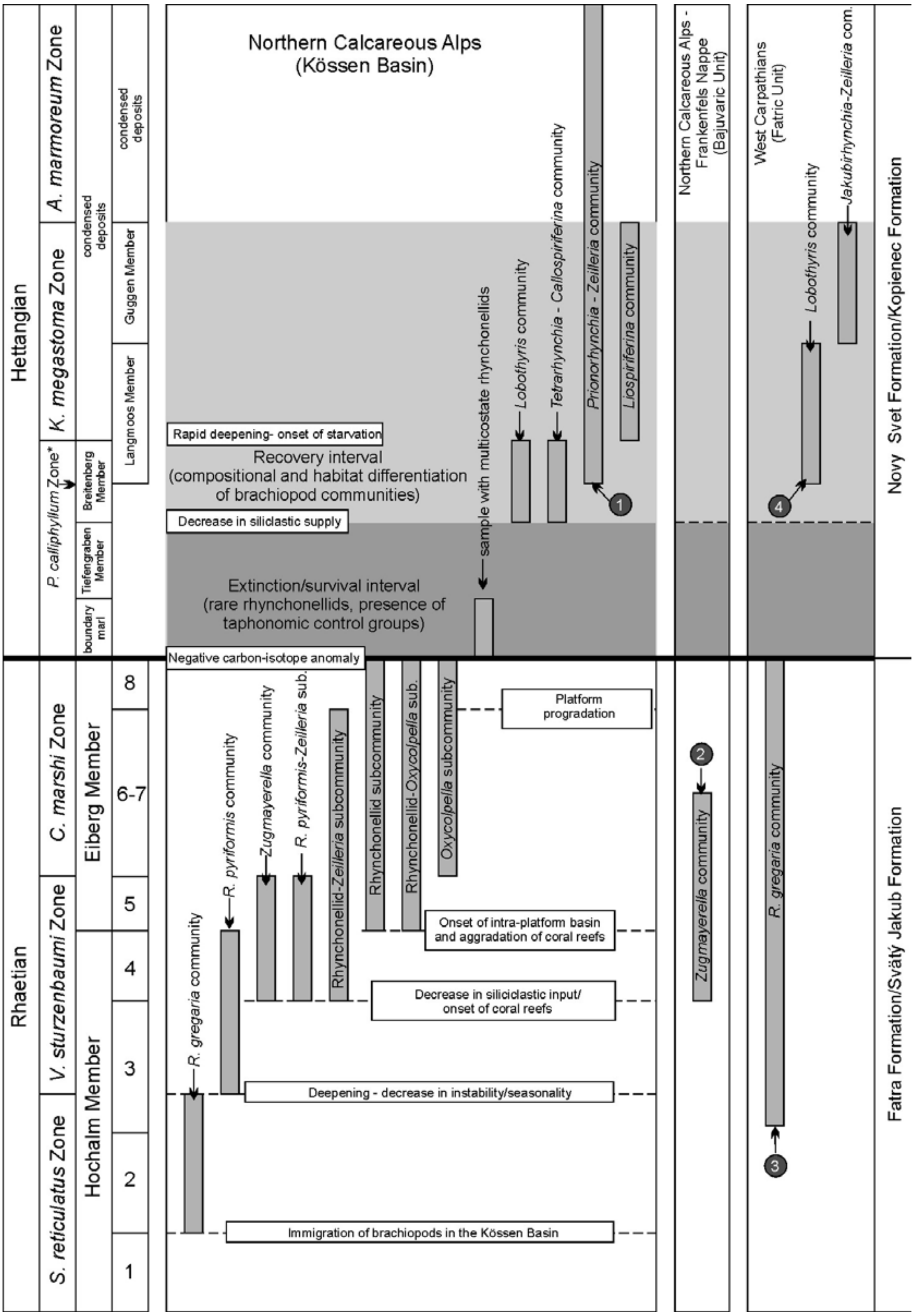


Figure 14 - Stratigraphic distribution of brachiopod communities at the TJB in the Kössen Basin. Note that the *R. gregaria* and *Zugmayerella* communities persisted to the *C. marshi* Zone in the Frankenfels Nappe (Bajuvaric Unit) and in the West Carpathians. Each zone has the equal column height which does not correspond to the stratigraphic thickness or age span. Litho- and biostratigraphic units are not to scale. * - the *P. calliphyllum* Zone is restricted to the Breitenberg Member. 1 – The first appearance of this community is represented by the dyke infill (*P. calliphyllum* Zone). The dyke is tentatively correlated with the Langmoos Member. 2 – The age is determined by conodonts as the *C. marshi* Zone (Golebiowski, 1990). 3 – The age of its appearance is not precisely known. The community ranges to the top of the Fatra Formation. 4 – The age of the first appearance is the Early or Middle Hettangian. The *Jakubirhynchia-Zeilleria* community is dated by an ammonite to the Middle Hettangian (Tomašových and Michalík, 2000).

Similarly as in the NCA, *Lobothyris* dominated in calcareous sand deposits originating in shallow habitats above NSWB in the Southern Alps and Transdanubian Central Range (TCR) (Gaetani, 1970; Dulai, 1993a, b, 2003). *Lobothyris* also dominated in offshore habitats below MSWB in the Lower and Middle Hettangian deposits of the West Carpathians (Tomašových and Michalík, 2000). *Lobothyris* belongs to the first brachiopod colonizers in the Hettangian deposits. Some features may indicate that *Lobothyris* belongs to taxa with opportunistic tendencies. This possibility might be indicated by its high community-level abundance and the occurrence in parautochthonous, loosely or densely packed shell beds, which can indicate rapid population turnover. Its abundance in habitats above NSWB might indicate that it tolerated some fluctuations in rate of sedimentation, nutrient supply or substrate stability. However, *Lobothyris* was well established in normal marine habitats in later Early Jurassic (Hallam, 1961; Tchoumatchenco, 1972, 1993; Aberhan 1992; Gahr, 2002) and does not occur in the high-stress habitats in the aftermath of mass extinction or in marginal unstable habitats during “background” times.

The communities dominated by rhynchonellids and *Zeilleria* have also compositional counterparts in the Hettangian of the West Carpathians (Tomašových and Michalík, 2000) and Southern Alps (Gaetani, 1970), and in the Sinemurian of the NCA and TCR. Similarly as in the Hettangian of the NCA, these typically occur in carbonate habitats with minimum siliciclastic input and reduced sedimentation rate. Dulai (1990) and Vörös et al. (2003) described assemblages of Sinemurian age dominated by *Zeilleria*, *Liospiriferina* and rhynchonellids such as *Prionorhynchia* and *Cirpa*. Communities dominated by *Tetrarhynchia* and *Saubachia* may be comparable to those with common rhynchonellids typical of siliciclastic habitats below MSWB, which are typical of the Early Jurassic habitats of NW Europe (e.g, *Calcirhynchia* dominates in siliciclastic offshore deposits, Hallam, 1960; Alméras and Hanzo, 1991).

Rhaetian vs. Hettangian brachiopod communities

Hypothesis 1 - composition of Rhaetian vs. Hettangian brachiopod communities

Analytical approach. Evaluating community turnover during mass extinctions, it is important to distinguish between local turnovers caused by habitat tracking, basin-scale immigration/local extinction and within-lineage replacement, and turnovers due to a real extinction of dominant taxa that leads to a change in phylogenetic structure of communities (Webb et al., 2002). Habitat tracking can lead to artifactual turnover if a temporal change is associated with an environmental change and the compared time intervals record different habitats. This problem can be accommodated by comparing equivalent parts of onshore-offshore gradients (Smith et al., 2001). The comparison of onshore-offshore gradient in the Kössen Basin between the Rhaetian and the Hettangian is limited. In contrast to the Rhaetian, coral patch-reefs were completely missing in the Hettangian of the NCA. During the Hettangian, carbonate deposition with much reduced sedimentation rate due to starvation is typical of some habitats below MSWB. Such habitats do not have comparable counterparts in the Rhaetian. However, the Rhaetian and Hettangian deposits record mixed carbonate-siliciclastic habitats with equivalent depths and can be generally comparable. Effects of local extinction can be understood using data from adjacent geographic areas. For the Kössen Basin, the significant differences in generic composition among Rhaetian zones and among Hettangian zones are mainly caused by local extinctions and immigrations. The communities which lived in the Kössen Basin during the Early Rhaetian tracked their habitats beyond the Kössen Basin during the Late Rhaetian. Effects of within-lineage replacement can be partly accommodated by evaluating turnover on several taxonomic levels. Although explicit phylogenetic analyses of Triassic and Jurassic brachiopods are not available, this approach assumes that higher-order taxonomic categories above the generic level reflect biologically-meaningful units (Carlson, 1991; Sepkoski and Kendrick, 1993).

We use one-factorial ANOSIM as the method for estimating the compositional turnover at the TJB (e.g., Pandolfi, 1996; Bonuso et al., 2002). Theoretically, there can be a substantial compositional change in benthic communities without invoking any mass extinction event (e.g., coordinated turnover, Boucot, 1983; Brett and Baird, 1995; Sheehan, 1996; Ivany, 1996; Patzkowsky and Holland, 1997; Olszewski and Patzkowsky, 2001; DiMichele et al., 2004). However, a mass extinction event can be supposed to be an end-member along a turnover continuum because an environmental disturbance is supposed to be an important agent causing the coordinated turnover. In order to estimate the compositional turnover at the TJB, we extend the approach used in testing of "coordinated stasis" by two inter-related approaches. First, in order to evaluate intensity of turnover, ANOSIM compares the Rhaetian and Hettangian communities on several taxonomic levels. Second, R values that reflect compositional turnover between stratigraphic zones are compared within the Rhaetian and within the Hettangian with an R value at the TJB. This approach thus enables to estimate if the intensity of turnover between the Rhaetian and Hettangian is indeed higher than during "background" times.

Evaluating compositional turnover in community-level abundance of taxa on several taxonomic levels can be a robust measure of ecologic impact of mass extinction. Any survivors passing through the mass extinction will depress the extinction rate which is supposed to be a main measure of evolutionary impact. However, that these survivors do not re-attain their previous community-level abundance is obviously of ecologic importance. This information is missed by taxonomic rate metrics or taxonomic diversity measures (Foote, 2000). This measure should be also not strongly affected by sampling and preservation biases that influence diversity comparisons because it is based on relative abundances.

	R - genera	p-value	R - families	p-value	R - superfamilies	p-value	R - suborders	p-value	R - orders	p-value
Comparison of stages:										
Rhaetian vs. Hettangian	0.487	<0.0001	0.606	<0.0001	0.497	<0.0001	0.016	0.36	-0.056	0.81
Comparison of zones:										
K. megastoma Zone vs. *A. marmoreum* Zone	0.282	(0.24)	0.3	(0.24)	0.309	(0.24)	-0.164	(0.57)	-0.145	(0.57)
P. calliphyllum Zone vs. *K. megastoma* Zone	0.534	0.007	0.455	0.01	0.384	0.019	0.255	0.052	0.229	0.061
C. marshi **Zone vs.** ***P. calliphyllum*** **Zone (T-J)**	**0.935**	**<0.0001**	**0.949**	**<0.0001**	**0.792**	**<0.0001**	**0.563**	**<0.0001**	**0.466**	**<0.0001**
V. sturzenbaumi Zone vs. *C. marshi* Zone	0.568	<0.0001	0.568	<0.0001	0.568	<0.0001	0.547	<0.0001	0.56	<0.0001
S. reticulatus Zone vs. *V. sturzenbaumi* Zone	0.278	0.005	0.285	0.005	0.285	0.005	0.336	0.001	0.083	0.17
Comparison of Rhaetian units:										
Rhaetian Unit 8 vs. ***P. calliphyllum*** **Zone (T-J)**	**0.828**	**0.0003**	**0.891**	**0.0001**	**0.717**	**0.0005**	**0.507**	**0.003**	**0.58**	**0.001**
Rhaetian Unit 6-7 vs. Rhaetian Unit 8	0.008	0.375	0.008	0.379	0.008	0.38	0.022	0.312	0.013	0.343
Rhaetian Unit 5 vs. Rhaetian Unit 6-7	0.153	0.054	0.153	0.051	0.153	0.052	0.145	0.064	0.096	0.131
Rhaetian Unit 4 vs. Rhaetian Unit 5	0.287	0.007	0.286	0.007	0.286	0.006	0.298	0.006	0.345	0.002
Rhaetian Unit 3 vs. Rhaetian Unit 4	0.155	0.113	0.162	0.103	0.162	0.102	0.151	0.113	-0.099	0.801
Rhaetian Unit 2 vs. Rhaetian Unit 3	0.644	0.002	0.644	0.002	0.644	0.002	0.644	0.002	0.605	0.002

Table 3 - ANOSIM results showing differences in composition between Rhaetian and Hettangian samples at five taxonomic levels. Note that the highest turnovers on genus, family and superfamily levels occurred at the TJB boundary (in bold). The p-values in parentheses are inconclusive due to low number of permutations.

Results. ANOSIM demonstrates that the Rhaetian and Hettangian brachiopod communities are significantly different in composition on the generic level (R = 0.49, $p<0.0001$; Fig. 15, Table 3). One genus (*Zeilleria*) crossed the T/J boundary in this area. If the generic assignment of ?*Calcirhynchia subrimosa* is supported, this genus will also belong to survivors because it is reported from the Hettangian of the western Tethys. However, it was mainly abundant during the Hettangian in the NW European province. In addition, there are significant differences between the Rhaetian and Hettangian communities on the family and superfamily level (Fig. 15, Table 3). The superfamily Zeillerioidea and rhynchonellids belonging to the superfamilies Hemithiridoidea and Rhynchotetradoidea persisted into the Hettangian. One Hettangian sample dominated by *Tetrarhynchia* (superfamily Hemithiridoidea) groups together with the Rhaetian samples in NMDS based on superfamily-level abundances. The differences between Hettangian and Rhaetian communities disappear on suborder and order levels (Fig. 15). Therefore, the compositional turnover at the TJB took place on the superfamily level.

ANOSIM also shows that the compositional turnover of brachiopod communities on generic level at the TJB (R = 0.94) is substantially higher than turnovers between the Rhaetian zones (R = 0.27-0.57) and between the Hettangian zones (R = 0.28-0.53). Note that the difference is even more pronounced when compositional differences are estimated among the Rhaetian units (Table 3). Although this test is conservative because it does not take into account the samples from other regions where some communities migrated during Late Rhaetian, it shows that turnover at the end of the Rhaetian was of higher magnitude than within-Rhaetian turnovers. The same pattern is visible on the family and superfamily level (Table 3). On the suborder and order level, the difference between the *V. sturzenbaumi* and *C. marshi* zones is comparable to the difference at the TJB. This pattern is mainly caused by differential proportions of athyridids and spiriferinids between the *V. sturzenbaumi* and *C. marshi* zones. With the exception of a strong difference between units 2 and 3 (*R. gregaria* is the only brachiopod in Unit 2), the differences between the Rhaetian units (R = 0.008-0.28) contrast with the turnover at the TJB (R = 0.83).

Discussion. The significant compositional turnover on superfamily level implies that the TJB event had substantial consequences on community ecology of Jurassic brachiopods. This event changed the phylogenetic structure of brachiopod communities (Fig. 16). Although there are yet no consistent data on long-term compositional changes of Jurassic brachiopod communities, it seems that this changeover in the dominance on the superfamily level had long-standing effects on the composition of brachiopod communities. Brachiopod communities comparable in composition to those in the Hettangian are typical of the Early Jurassic (e.g., Manceñido and Owen, 2001).

The Rhaetian brachiopods that were numerically abundant in local communities belong to extinct athyridoids, spondylospiroids and dielasmatoids (Fig. 16). Zeillerioids were abundant in both Rhaetian and Hettangian communities. In contrast, the Hettangian dominants belong to spiriferinoids, pennospiriferinoids and terebratuloids which were rare in the Rhaetian (Fig. 16). Evaluation of rhynchonellid turnover is obscured by taxonomic inconsistencies and lack of explicit phylogenetic framework, but rhynchonelloids, wellerelloids and rhynchotetradoids are known to be abundant in the Jurassic communities, in spite of their rarity in the Late Triassic. Note that this pattern does not follow from stratigraphic ranges of brachiopod superfamilies. Spiriferinoids, zeillerioids and rhynchotetradoids occur both in Rhaetian and Hettangian, but their community-level abundance and co-existence with other superfamilies differ.

Most of the short-looped terebratulids which have dominated in Triassic communities belong to dielasmatoids (e.g. *Coenothyris* in the Middle Triassic, *Cruratula* and *Rhaetina* in Late Triassic). One exception is represented by endemic plectoconchid terebratuloids *Plectoconcha* and *Pseudorhaetina*. They were locally abundant in Late Triassic shallow habitats of the Eastern Pacific region (Sandy and Stanley, 1993; Stanley et al., 1994).

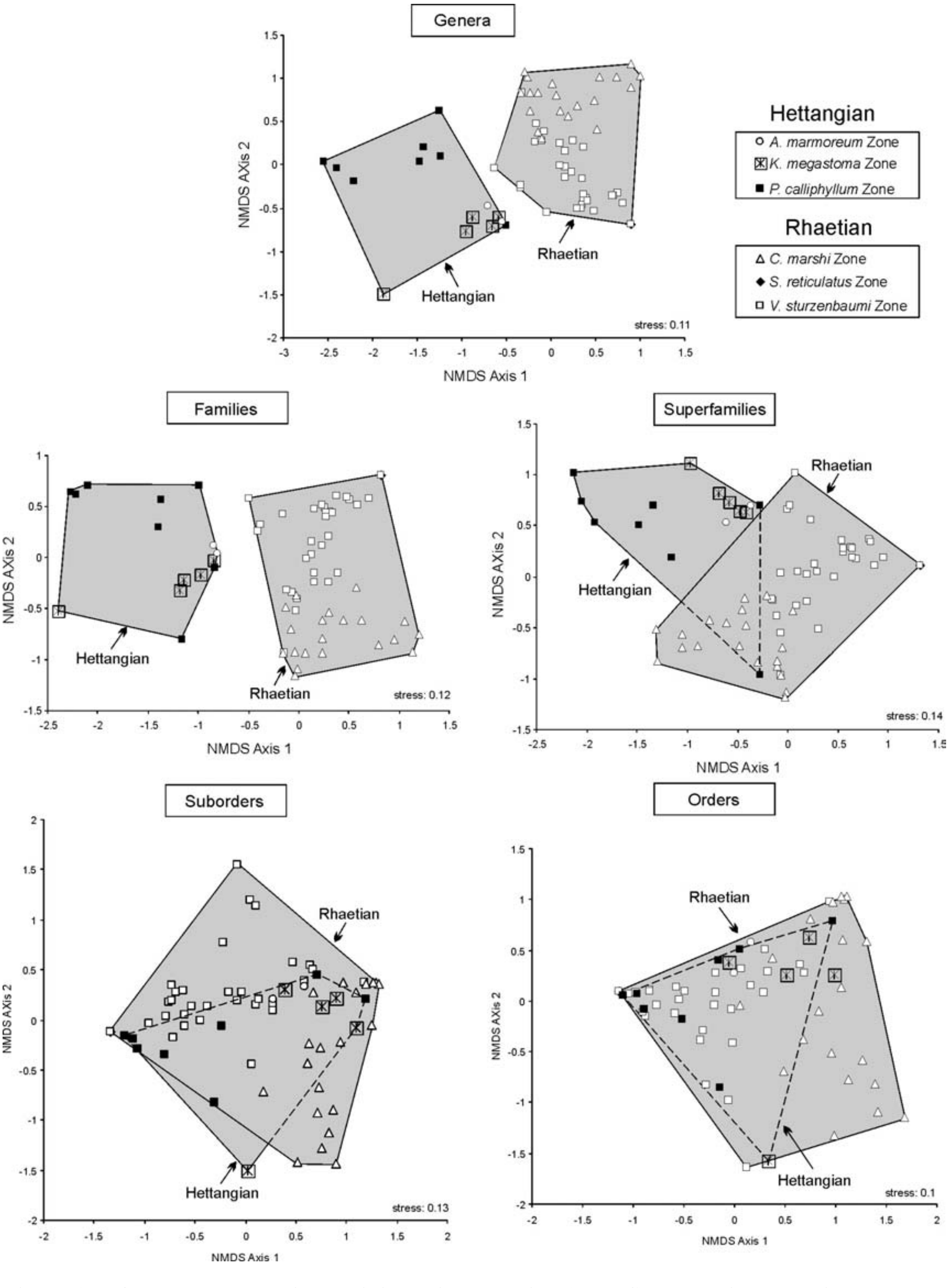


Figure 15 - Q-mode non-metric multidimensional scaling (NMDS) comparing Rhaetian and Hettangian samples at five taxonomic levels. The configurations are rotated to have the greatest variation along the first axis for visual convenience. Note that the segregation persists up to the superfamily level. Rhaetian "rhynchonellids" were assigned to the family Cyclothyrididae and superfamily Hemithiridoidea.

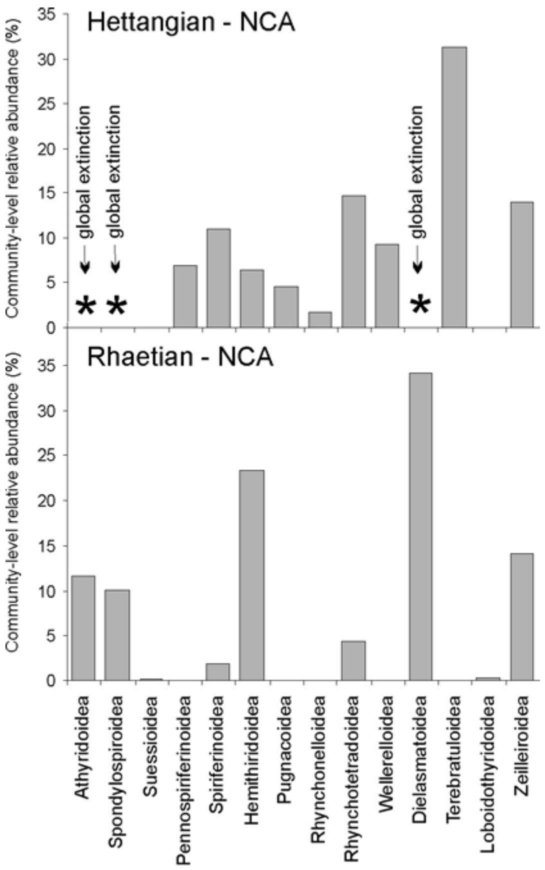


Figure 16 - The change in community-level abundances of superfamilies after the TJB in the NCA. It demonstrates the effect of the end-Triassic mass extinction on the composition of the post-extinction brachiopod communities. The relative abundances are based on pooled relative abundances of all samples. Note that the superfamilies Athyridoidea, Spondylospiroidea and Dielasmatoidea went globally extinct at the TJB.

Although Late Triassic terebratuloids are not represented in our dataset, they are rare in the Norian and Rhaetian deposits of the NCA. For example, *Lobothyris* occurs in the Carnian limestones of the Brock Mountain in California (Sandy, 2001) and is a subordinate component of brachiopod communities from Norian deposits of the NCA and Rhaetian deposits of the West Carpathians (Siblík, 1967). Therefore, the dominance of dielasmatoids was typical of the Triassic communities. In contrast, terebratuloids with *Lobothyris* were numerically abundant in the Early Jurassic communities.

Spiriferinids on the ordinal or subordinal level decreased in the diversity during the Early Jurassic and finally went extinct in the Early Toarcian (Ager, 1987). Jablonski (2001) supposed that they are an example of dead clade walking (i.e., survival without recovery, leading to decline in the aftermath of mass extinction) after the TJB. However, spiriferinoids and pennospiriferinoids were abundant in some Early Jurassic brachiopod communities (Aberhan, 1992; Gahr, 2002), in contrast to their rarity in Triassic communities. On superfamily level, spiriferinoids and pennospiriferinoids were probably less affected by extinction than spondylospiroids because their community-level abundance increased after the TJB.

The lower levels of the turnover between the Rhaetian zones and between the Hettangian zones demonstrate that the turnover at the TJB was rather abrupt (i.e., restricted to the interval between the uppermost parts of the Kössen Formation and the *P. calliphyllum* Zone). This turnover is not related to prolonged extinctions throughout the Late Triassic that were assumed by Hallam (2002) and Lucas and Tanner (2004). In addition to the measure of the compositional turnover, from 21 brachiopod species known from more than one occurrence in the NCA, at least 14 species range to the uppermost part of the Rhaetian deposits in this area (Unit 8 of the Eiberg Member, see Mostler et al., 1978; Golebiowski, 1990; Siblík, 1998). Although some rhynchonellid superfamilies and zeillerioids may show pseudo-extinction, none of these 14 species crosses the TJB. The data about some Early Jurassic survivors (e.g., species of *Rhaetina, Zugmayerella* and *Fissirhynchia*) are either unsupported by stratigraphic data or determined without diagnostic criteria. If such findings will eventually be proven, such survivors will rather belong to dead clade walkers (Jablonski, 2002), indicating immediate consequence of the end-Triassic mass extinction.

Hypothesis 2 - environmental preferences of Rhaetian vs. Hettangian brachiopods

The second hypothesis tests whether environmental distribution of brachiopods did substantially change after the TJB. Sandy (1995) hypothesized that brachiopod suborders/orders show differential environmental preferences before and after the end-Triassic mass extinction, partly as a consequence of vacated deep habitats after the extinction of athyridoids. He hypothesized that rhynchonellids became to be more abundant in shallow, high-energy habitats, in contrast to their deep water preference in the Rhaetian. In contrast, short-looped terebratulids were typical of shallow water habitats in the Rhaetian, but changed their preference to deeper waters in the Early Jurassic. Spiriferinids and long-looped terebratulids (suborder Terebratellidina) shifted to the deepest parts of transect during the Early Jurassic.

We evaluate the hypothesis with help of time-environment diagrams using relative abundances of orders/suborders in three depth habitats (Fig. 17). The predictions of Sandy with respect to the expected change in environmental distribution are not met by Hettangian rhynchonellids and short-looped terebratulids (suborder Terebratulidina). Several rhynchonellids dominated in relatively deep habitats below MSWB during the Hettangian. In addition, some rhynchonellids were common in shallow habitats during the Rhaetian. Short-looped terebratulids were abundant in shallow habitats above NSWB both in the Rhaetian and Hettangian. This distribution is in accord with the observations from the TCR where *Lobothyris* dominated in shallow habitats during the Hettangian (Dulai, 2003). Dulai (2003) suggested that the change in depth distribution of short-looped terebratulids predicted by Sandy took place after the Hettangian in the western Tethys. Alternatively, the shift of short-looped terebratulids towards deeper habitats might be related to their differential environmental preference at family level (Sandy, 1995). Smooth and sulcate terebratulids belonging to the family Nucleatidae (e.g., *Linguithyris, Securithyris* and *Phymatothyris,* Manceñido, 1993) were typical of carbonate-starved Tethyan habitats and commonly occurred in deep habitats below MSWB in the Early Jurassic (Vörös, 1986, 2005).

Although the depth distribution of short-looped terebratulids and rhynchonellids did not change after the end-Triassic mass extinction in the NCA, long-looped terebratulids and spiriferinids seem to show the predicted shift towards deeper habitats after the end-Triassic mass extinction (Fig. 17). After the extinction of Athyrididina, both suborders were relatively common in habitats below MSWB during the Hettangian, in contrast to their higher abundance in shallower habitats during the Rhaetian. However, the missing data about the Middle and Late Hettangian shallow habitats are needed for confirmation of their distributional shift.

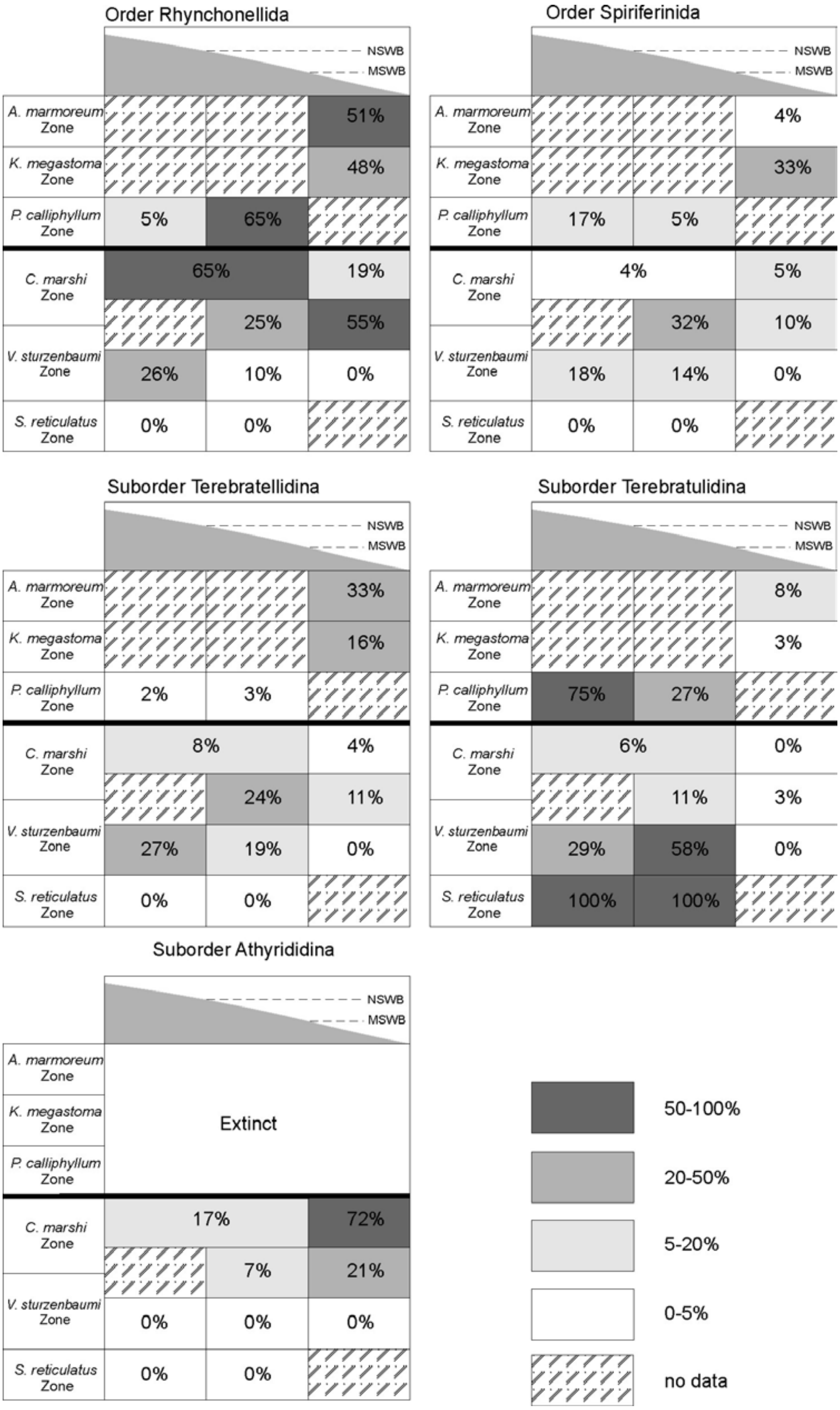


Figure 17 - Time-environment diagrams of five suborders/orders. Note that short-looped terebratulids occupied shallow habitats both in the Rhaetian and Hettangian and rhynchonellids were generalistic in distribution. Long-looped terebratulids and spiriferinids may indicate shift to deeper habitats after the end-Triassic mass extinction event.

Conclusions

(1) The extinction-survival interval, which is marked by the several meters thick boundary marl with distinct geochemical, sedimentologic and palynofacies features at the base of the Kendlbach Formation (TJB), contains rare rhynchonellid brachiopods. A relatively rapid recovery during late Early and Middle Hettangian is indicated by the presence of several brachiopod communities that differ in their depth and substrate preferences and by their relatively high beta diversity.

(2) The significant differences in composition of Rhaetian and Hettangian communities on superfamily level demonstrate that the end-Triassic mass extinction had substantial ecologic effects on brachiopods. With the exception of zeillerioids and some rhynchonellid superfamilies, dominant brachiopods of the Rhaetian communities belonged to superfamilies that went extinct on the TJB. In contrast, the dominants of the Hettangian communities belonged to spiriferinoids, pennospiriferinoids, terebratuloids and rhynchotetradoids that were subordinate in Rhaetian communities. The end-Triassic extinction thus re-directed and constrained the composition of Jurassic brachiopod communities. This study thus highlights the role of large-scale physical perturbations in mediating biotic replacements. Measuring turnover in terms of community-level abundance of taxa during mass extinctions should be highly relevant as taxonomic extinction rate metrics miss the information about their community-level abundance.

(3) Although some brachiopod communities occur in the lower part of the Kössen Formation only, they are present in other regions adjacent to the Kössen Basin up to the Late Rhaetian. This implies relatively high persistence of brachiopod communities during the Rhaetian. Analyses of similarities demonstrate that the compositional turnover of brachiopod communities on genus level at the TJB ($R = 0.94$) is substantially higher than the turnovers within the Rhaetian ($R = 0.28$-0.57) and within the Hettangian ($R = 0.28$-0.53). This pattern indicates a rather abrupt turnover that took place between the uppermost parts of the Kössen Formation and the lower parts of the Kendlbach Formation.

(4) Time-environment diagrams indicate that the environmental distribution of brachiopods on suborder/order level did not substantially change after the TJB in the NCA. Although long-looped terebratulids and spiriferinids showed the increase in their depth range, short-looped terebratulids were still common in shallow habitats and rhynchonellids were generalists both during the Rhaetian and the Hettangian.

Sample ID (G-Golebiowski, S-Siblik, T-Tomasovych)	Section	*Rhaetina gregaria*	*Rhaetina pyriformis*	*Zeilleria*	*Zugmayerella*	*Sinucosta*	Rhynchonellids	*Oxycolpella*	*Austrirhynchia*	*Laballa*	*Triadithyris*
S-HM	Hoher Mandling	8	9	6	5	0	13	0	0	0	0
S-KI	Kitzberg	2	8	3	12	0	0	0	0	0	0
G-EB30	Eibenberg	1	13	5	3	0	0	0	0	0	0
G-E14	Eiberg	0	0	17	8	8	51	36	0	0	0
G-E21	Eiberg	0	0	11	6	5	17	20	0	0	0
G-F2	Fonsjoch	0	0	0	0	2	5	23	0	0	0
G-F4	Fonsjoch	0	0	6	0	3	35	19	0	0	0
G-G8	Gaissau	0	9	0	3	0	0	0	4	0	0
G-H16	Hochalm	2	10	0	6	0	0	0	3	0	0
G-H25	Hochalm	0	15	3	3	0	31	0	0	0	0
G-KE111	Kendlbachgraben	0	9	11	5	0	20	4	0	0	0
G-KE119	Kendlbachgraben	0	0	5	0	0	9	18	0	0	0
G-K3	Kössen	0	0	3	6	0	9	0	2	0	0
G-K4	Kössen	0	18	8	0	0	0	0	3	0	0
G-N40	Neuhaus	3	7	0	6	0	0	0	2	0	0
G-OA32	Oberer Ampelsbach	0	21	9	4	0	0	0	0	0	0
G-SC2	Steinplatte	0	0	0	0	9	17	39	0	0	0
G-S84	Steinplatte	0	0	0	0	0	2	32	0	0	0
G-S2	Steinplatte	1	10	4	3	0	0	0	2	0	0
G-S1	Steinplatte	0	0	20	8	0	26	2	5	0	0
G-V13	Voralpe	3	17	0	1	0	0	0	5	0	0
T-E44	Eiberg	0	38	9	0	0	0	0	0	0	0
T-E79	Eiberg	0	0	0	1	0	77	0	0	0	0
T-E95	Eiberg	0	0	0	0	11	1	15	0	1	0
T-E101	Eiberg	0	0	0	3	0	3	35	0	0	0
T-E2-13	Eiberg	0	0	5	0	0	3	2	0	0	0
T-E2-20	Eiberg	0	0	0	4	3	25	0	0	0	0
T-E2-38	Eiberg	0	0	0	0	0	6	2	1	0	0
T-H30	Hochalm	0	10	0	0	0	0	0	0	0	0
T-H35	Hochalm	0	2	7	0	0	0	0	1	0	0
T-K4	Kössen	0	25	12	0	0	0	0	1	0	3
T-K9	Kössen	0	0	11	2	1	15	1	5	0	0
T-K11	Kössen	0	0	3	2	0	6	27	1	0	0
T-K12	Kössen	0	0	0	0	0	60	0	0	0	0
T-K13	Kössen	0	0	2	0	0	37	0	0	0	0
T-SA1	Steinplatte PRA	4	6	8	0	0	0	0	1	0	0
T-SA2	Steinplatte PRA	0	15	11	6	0	7	0	7	0	1
T-SC2	Steinplatte PRC	15	13	14	5	0	9	0	0	0	0
T-SC1	Steinplatte PRC	0	0	8	11	0	0	0	1	0	0
T-SC4	Steinplatte PRC	2	6	3	0	1	0	0	1	0	0
T-SC5	Steinplatte PRC	0	0	3	7	0	0	0	1	0	0
T-G2-3	Gaissau	0	0	4	3	0	5	0	0	0	0
T-G2-4	Gaissau	0	0	2	3	0	7	0	0	0	0
T-G9	Gaissau	0	0	5	0	0	83	0	0	0	0
S-AD	Adnet	0	0	7	2	0	43	0	3	0	0
S-RO	Rötelwand	0	0	4	0	0	241	0	115	0	0
S-SA	Steinplatte PRA	2	12	12	14	0	11	0	7	0	4
S-SB	Steinplatte PRB	0	3	2	1	0	5	0	1	0	1
S-KG1	Steinplatte-Kohrgatterl	2	25	35	6	0	12	0	5	0	1
S-P	Steinplatte-Plattenkogel	0	15	9	5	0	11	40	0	1	0
S-KG2	Steinplatte	0	15	19	3	12	10	15	0	0	0
S-KG3	Steinplatte	0	14	20	2	0	12	2	9	0	0
S-KG4	Steinplatte	0	1	8	149	0	3	1	0	0	0
T-H2	Hochalm	12	0	0	0	0	0	0	0	0	0
T-H3-1	Hochalm	81	0	0	0	0	0	0	0	0	0
T-H3-2	Hochalm	73	0	0	0	0	0	0	0	0	0
G-H3	Hochalm	15	0	0	0	0	0	0	0	0	0
T-H4	Hochalm	28	0	0	0	0	0	0	0	0	0
GH10	Hochalm	11	0	0	0	0	0	0	0	0	0
T-H13	Hochalm	22	0	0	0	0	0	0	0	0	0
G-H13	Hochalm	56	0	0	0	0	0	0	0	0	0
T-K1	Kössen	17	0	0	0	0	0	0	0	0	0

Supplement 1 – Absolute abundances of Rhaetian brachiopods used in multivariate analyses.

Sample ID (G-Golebiowski, S-Siblík, T-Tomašových)	Locality	Habitat	Zone	Unit	Source
S-HM	Hoher Mandling	no data	no data	no data	Siblík (unpublished)
S-KI	Kitzberg	no data	no data	no data	Siblík (unpublished)
G-EB30	Eibenberg	no data	*V. sturzenbaumi* Zone	4	Golebiowski (1989)
G-E14	Eiberg	below MSWB	*C. marshi* Zone	6	Golebiowski (1989)
G-E21	Eiberg	below MSWB	*C. marshi* Zone	6-7	Golebiowski (1989)
G-F2	Fonsjoch	below MSWB	*C. marshi* Zone	8	Golebiowski (1989)
G-F4	Fonsjoch	below MSWB	*C. marshi* Zone	6-7	Golebiowski (1989)
G-G8	Gaissau	below NSWB	*V. sturzenbaumi* Zone	3	Golebiowski (1989)
G-H16	Hochalm	below NSWB	*V. sturzenbaumi* Zone	3	Golebiowski (1989)
G-H25	Hochalm	below MSWB	*V. sturzenbaumi* Zone	5	Golebiowski (1989)
G-KE111	Kendlbachgraben	below MSWB	*V. sturzenbaumi* Zone	5	Golebiowski (1989)
G-KE119	Kendlbachgraben	below MSWB	*C. marshi* Zone	8	Golebiowski (1989)
G-K3	Kössen	below MSWB	*V. sturzenbaumi* Zone	5	Golebiowski (1989)
G-K4	Kössen	below NSWB	*V. sturzenbaumi* Zone	4	Golebiowski (1989)
G-N40	Neuhaus	below NSWB	*V. sturzenbaumi* Zone	3	Golebiowski (1989)
G-OA32	Oberer Ampelsbach	no data	*V. sturzenbaumi* Zone	4	Golebiowski (1989)
G-SC2	Steinplatte	below MSWB	*C. marshi* Zone	8	Golebiowski (1989)
G-S84	Steinplatte	below MSWB	*C. marshi* Zone	8	Golebiowski (1989)
G-S2	Steinplatte	no data	*V. sturzenbaumi* Zone	4	Golebiowski (1989)
G-S1	Steinplatte	below NSWB	*V. sturzenbaumi* Zone	5	Golebiowski (1989)
G-V13	Voralpe	below NSWB	*V. sturzenbaumi* Zone	3	Golebiowski (1989)
T-E44	Eiberg	below NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-E79	Eiberg	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-E95	Eiberg	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-E101	Eiberg	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-E2-13	Eiberg	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-E2-20	Eiberg	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-E2-38	Eiberg	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-H30	Hochalm	below NSWB	*V. sturzenbaumi* Zone	3	Tomašových (unpublished)
T-H35	Hochalm	below NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-K4	Kössen	below NSWB	*V. sturzenbaumi* Zone	3	Tomašových (unpublished)
T-K9	Kössen	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-K11	Kössen	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-K12	Kössen	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-K13	Kössen	below MSWB	*C. marshi* Zone	6-7	Tomašových (unpublished)
T-SA1	Steinplatte PRA	above NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-SA2	Steinplatte PRA	above NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-SC2	Steinplatte PRC	above NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-SC1	Steinplatte PRC	below NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-SC4	Steinplatte PRC	above NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-SC5	Steinplatte PRC	above NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-G2-3	Gaissau	above NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-G2-4	Gaissau	above NSWB	*V. sturzenbaumi* Zone	4	Tomašových (unpublished)
T-G9	Gaissau	below NSWB	*V. sturzenbaumi* Zone	5	Tomašových (unpublished)
S-AD	Adnet	above MSWB	*C. marshi* Zone	8	Siblík (1998)
S-RO	Rötelwand	above MSWB	*C. marshi* Zone	8	Siblík (1998)
S-SA	Steinplatte PRA	above NSWB	*V. sturzenbaumi* Zone	4	Siblík (1998)
S-SB	Steinplatte PRB	above NSWB	*V. sturzenbaumi* Zone	4	Siblík (1998)
S-KG1	Steinplatte-Kohrgatterl	above NSWB	*V. sturzenbaumi* Zone	4	Siblík (1998)
S-P	Steinplatte-Plattenkogel	above MSWB	*C. marshi* Zone	8	Siblík (1998)
S-KG2	Steinplatte	below NSWB	*V. sturzenbaumi* Zone	5	Turnsek et al. (1999)
S-KG3	Steinplatte	below NSWB	*V. sturzenbaumi* Zone	5	Turnsek et al. (1999)
S-KG4	Steinplatte	below NSWB	*V. sturzenbaumi* Zone	5	Turnsek et al. (1999)
T-H2	Hochalm	above NSWB	*S. reticulatus* Zone	2	Tomašových (unpublished)
T-H3-1	Hochalm	above NSWB	*S. reticulatus* Zone	2	Tomašových (unpublished)
T-H3-2	Hochalm	above NSWB	*S. reticulatus* Zone	2	Tomašových (unpublished)
G-H3	Hochalm	above NSWB	*S. reticulatus* Zone	2	Golebiowski (1989)
T-H4	Hochalm	below NSWB	*S. reticulatus* Zone	2	Tomašových (unpublished)
GH10	Hochalm	above NSWB	*S. reticulatus* Zone	2	Tomašových (unpublished)
T-H13	Hochalm	below NSWB	*S. reticulatus* Zone	2	Tomašových (unpublished)
G-H13	Hochalm	below NSWB	*S. reticulatus* Zone	2	Golebiowski (1989)
T-K1	Kössen	below NSWB	*S. reticulatus* Zone	2	Tomašových (unpublished)

Supplement 2 - Stratigraphic and environmental assignments to Rhaetian samples.

Section	*Jakubirhynchia*	*Callospiriferina*	*Cirpa*	*Cuneirhynchia*	*Dispiriferina*	*Furcirhynchia*	*Homoeorhynchia*	*Linguithyris*	*Liospiriferina*	*Lobothyris*	*Piarorhynchia*	*Prionorhynchia*	*Saubachia*	*Spiriferina*	*Tetrarhynchia*	*Zeilleria*
Vorderskopf	10	20	0	0	0	0	0	0	0	75	0	0	2	0	0	0
Mittenwald	0	0	0	0	0	0	0	0	0	70	1	0	3	0	0	0
Hochleitengraben	0	8	0	0	0	0	0	0	0	0	0	0	0	0	76	3
Saubachgraben	0	0	0	0	0	0	0	0	0	16	3	0	10	0	0	1
Breitenberg	0	0	0	0	0	0	0	0	1	80	0	0	0	0	0	2
Vorderer Ampelsbach	0	73	0	0	0	0	0	0	0	33	0	0	0	0	11	12
Eiberg	0	5	0	0	0	0	0	0	0	65	0	0	1	2	0	0
Steinplatte	11	0	5	2	0	3	0	10	5	3	1	6	0	0	0	20
Hohes Brett	0	0	3	0	0	0	0	0	0	0	0	13	0	0	0	14
G. Langmoos Q.	5	3	44	0	0	0	0	0	12	3	0	64	0	0	0	18
W of Q. 28	1	0	2	0	3	0	0	0	31	0	0	1	0	0	0	0
Schnöll Q. 8	2	0	4	0	0	0	0	0	8	0	0	12	0	0	0	8
Schnöll Q. 9	1	0	2	0	0	0	0	0	8	0	0	8	0	0	0	1
Pooled Schnöll Q. 5	1	1	4	0	0	0	0	4	0	0	0	9	0	0	0	12
Pooled Adnet	4	0	2	1	0	0	0	1	0	0	0	3	0	0	0	6

Supplement 3 - Absolute abundances of Hettangian brachiopods used in multivariate analyses.

Section	Zone	Formation	Habitat/facies	Source
Vorderskopf	*P. calliphyllum* Zone	Kendlbach Formation	Above NSWB	Siblík (1993)
Mittenwald	*P. calliphyllum* Zone	Kendlbach Formation	Above NSWB	Böhm et al. (1999)
Hochleitengraben	*P. calliphyllum* Zone	Kendlbach Formation	Above MSWB	Böhm et al. (1999)
Saubachgraben	*P. calliphyllum* Zone	Kendlbach Formation	Above MSWB	Böhm et al. (1999)
Breitenberg	*P. calliphyllum* Zone	Kendlbach Formation	Above NSWB	Tomašových (unpublished)
Vorderer Ampelsbach	*P. calliphyllum* Zone	Kendlbach Formation	Above NSWB	Tomašových (unpublished)
Eiberg	*P. calliphyllum* Zone	Kendlbach Formation	Above NSWB	Siblík (1998)
Steinplatte	*A. marmoreum* Zone	Enzesfeld Limestone	Below MSWB	Kment, Morawetz and Siblík (unpub.)
Hohes Brett	*P. calliphyllum* Zone	Dyke in Dachstein Fm	Below MSWB	Siblík (1999)
G. Langmoos Q.	*K. megastoma* Zone	Schnoll Formation	Below MSWB	Siblík (1999)
W of Q. 28	*K. megastoma* Zone	Schnoll Formation	Below MSWB	Siblík (1999)
Schnöll Q. 8	*K. megastoma* Zone	Schnoll Formation	Below MSWB	Siblík (1999)
Schnöll Q. 9	*K. megastoma* Zone	Schnoll Formation	Below MSWB	Hillebrandt (unpublished)
Pooled Schnöll Q. 5	*K. megastoma* Zone	Schnoll Formation	Below MSWB	Siblík (1999)
Pooled Adnet	*A. marmoreum* Zone	Enzesfeld Limestone	Below MSWB	Siblík (1999)

Supplement 4 - Stratigraphic and environmental assignments to Hettangian samples.

7. Brachiopod dominance in habitats with reduced competition for space: inference from relationship between shelly encrusters and benthic microbial communities (Lower Jurassic, Morocco)

(with M. Wilmsen and Franz T. Fürsich)

Abstract. Phases of extensive distribution of microbial carbonates in the fossil record are either explained by a decreased rate of their destruction via decreased intensity of competition and grazing and/or by an unusually high rate of production due to high alkalinity or other physical factors that increase calcification rates. In this chapter, intensity of competition for space and effects of shelly encrusters on microbial crusts are examined in Lower Jurassic predominantly heterotrophic, sponge-microbial communities of the Central High Atlas (Morocco). The sponge-microbial biostromes inhabited a fault-dissected ramp above and below maximum storm wave base. Absence of light-dependent encrusters, algae and microborers indicates limited light penetration in relatively shallow environments above storm wave base. Cementing bivalves decrease in abundance and microbial crusts increase in abundance and thickness towards the deeper environments. Encrusters and epibionts show distinct substrate preferences, with bivalves and serpulids dominating on sponge substrates and bryozoans and brachiopods dominating on microbial crusts. Significantly negative correlation between thickness of microbial crust and abundance of bivalves and serpulids, and significantly lower percent cover of shelly encrusters on microbial crusts than on sponge substrates indicate that the density of shelly encrusters and competition for space was lower in environments with microbial crusts. The hypothesis stating that distribution of microbial crusts correlates negatively with increasing competition for space is thus supported. This implies that brachiopods and bryozoans that preferentially inhabited microbial substrates had lower interference competitive abilities when compared to bivalves and serpulids. Separation of temporal and spatial factors demonstrates that both had significant effect on intensity of competition and abundances of the main biotic groups. Negative relationship between decreasing abundance of shelly encrusters and rising of the wave-base level through time implies a combined effect of biotic and abiotic factors on the distribution of benthic microbial communities. The decrease in storm activity might have been coupled with restricted water mixing and decreased oxygen concentrations, which would decrease competitive abilities of shelly encrusters and enhance growth potential of microbial crusts.

Introduction

Fossil benthic microbial communities, commonly associated with siliceous sponges or corals, produced unique and widespread and very thick carbonate-rich deposits during several Phanerozoic time intervals (Burne and Moore, 1987). During the Mesozoic, they were extensively developed mainly in the Late Jurassic (Keupp et al., 1990; Leinfelder et al., 1993; Brunton and Dixon, 1994). Two basic groups of mutually not exclusive hypotheses were proposed for explaining the spatial and temporal peaks in distribution of microbial carbonates in marine habitats (Riding 2000). First, the variations in extrinsic, abiotic factors related to increased seawater alkalinity due to the H_2S alkalinity pump (Kempe et al., 1996; Arp et al. 2001) or increased weathering of silicates (Reitner, 1993; Neuweiler, 1993) are implicitly assumed to substantially increase rate of calcification related directly or indirectly to microbial activity. Second, it was suggested that the extensive development of microbialites is enabled by the exclusion of their grazers and superior metazoan competitors, leading to a decrease in destruction rate of microbial mats or stops their growth inhibition (Riding, 2000). The proliferation of microbial communities is thus typically related to eutrophic, oxygen deficient or aphotic conditions that do not support most of the metazoan competitors of microbial crusts. It is invoked that this microbial dominance indicates an ecosystem collapse and biotic crisis in carbonate depositional systems that leads to an expansion of refugia-restricted microbial communities into habitats with a lower biotic pressure (Schubert and Bottjer, 1992; Whalen et al., 2002). The second hypothesis thus assumes that the intensity of biotic interactions decreased in the habitats dominated by microbial communities. Although biotic interactions are difficult to directly demonstrate in fossil and present-day communities, this hypothesis can be evaluated by estimating whether the observed difference in abundance of encrusting and grazing metazoans between microbial and non-microbial carbonates distribution is in accord with its prediction. The prediction is that the abundance of encrusters and grazers, all other factors being equal, is higher in communities with less abundant crusts than in habitats with more abundant microbial crusts. Distinguishing the effects of increased calcification rate, irrespective of competitive interactions on one hand and inhibition or destruction rate of microbial mats due to biotic effects on the other hand, is one of the main tasks in understanding the sedimentology and paleobiology of benthic microbial communities (Riding, 1997, 2000). If the data support the hypothesis of reduced competition intensity in microbial communities, metazoans preferring such communities can be also thought as less superior competitors for space in comparison to those that dominate in non-microbial communities.

Two goals are addressed in this chapter. First, the hypothesis that microbial communities signs environments with reduced competition for space and grazing is evaluated by analyzing the relationship between shelly encrusters and microbial crusts in one of the earliest known Jurassic ecosystems with microbial-sponge communities (Neuweiler et al., 2001). These communities are preserved as biostromes of uniform thickness in the Central High Atlas in the lower part of the Upper Sinemurian Foum Zidet Formation (Mehdi et al., 2003). The upper part of this formation is formed by large-scale, several meters or decameters thick sponge-microbial mounds that were described by Neuweiler et al. (2001). In order to evaluate the intensity of competition for space in microbial and non-microbial communities, variations in environmental factors related to sedimentation rate, land-derived nutrient supply, and water energy need to be minimal. These requirements can be partly fulfilled because the lower part of the Foum Zidet Formation contains a minimum amount of siliciclastics and reflects relatively comparable conditions in terms of background water-energy levels. Second, it is evaluated whether benthic metazoans differ in their environmental preferences with respect to abundance of microbial crusts. As will be shown, brachiopods and bivalves differ in abundance between environments with and without microbial communities, indicating their differential abilities with respect to competition for space.

Methods

Thirty-one thin-sections from the lower member of the Foum Zidet Formation were analyzed with respect to volumetric abundances of their components, estimated by semi-quantitative visual methods (Schäfer 1969). A cluster analysis was used for identification of facies types with similar component abundances and for identification of sample groups with similar abundances of encrusters. Q-mode and R-mode non-metric multidimensional scaling based on the Bray-Curtis similarity (BC) was used for assessing the relationship between samples, components and encrusters. Oysters, bryozoans and serpulids that were not attached to any substrate or were preserved as fragments were also assigned to encrusters. One-way analysis of similarities (ANOSIM) was used for evaluating whether there are differences in component abundances among environments and whether there are differences in encruster abundances among substrate types. In addition, 95% bootstrapped confidence intervals were computed for evaluating between-environment and between-substrate differences in component abundances. Two-way crossed ANOSIM was used for separating of temporal and environmental effects on component abundances. Spearman rank correlation coefficient was used for estimating the relationship between the mean thickness of microbial crusts and log-transformed abundance of components. The mean thickness and component abundances were normalized to Z-scores, which represent a measure of the distance in standard deviations of a sample from the mean, because their measurement scales are not comparable. 15-30 randomly selected components of each thin-section were measured for the estimation of mean thickness of microbial crusts. The crust thickness was measured as an average thickness of two external crusts that coated components on their opposite sides. Microbial infillings of shells or skeletal pores with internal crusts were not measured.

Sections

Two sections at Foum Zidet (Fig. 1) that expose an about 60 m-thick lower member of the Foum Zidet Formation (*Asteroceras obtusum* Zone, lower Upper Sinemurian) consist of dark-colored, well-bedded, micrite-rich limestone beds with abundant microbialites, sponges, and level-bottom epibenthic fauna and with a minimum amount of siliciclastic sediments (Wilmsen et al., 2002; Mehdi et al., 2003). They are situated in the Rich area of the Central High Atlas and represent deposits of the hanging wall of the Rich fault-block. The lower member of the Foum Zidet Formation is overlying laminated, micritic or fenestrae-bearing mudstones and wackestones of the Idikel Formation (Lower Sinemurian). The middle member is composed of a relatively uniform alternation of argillaceous mudstones and marls containing rare cherts and sponge debris. The upper member of the Foum Zidet Formation is formed by several meters-thick microbial-sponge mounds and inter-mound, well-bedded mudstones and wackestones with sponge, brachiopod and oyster debris (Neuweiler et al., 2001). The upper part of the Foum Zidet Formation is terminated by a Fe-rich hardground that is overlain by the hemipelagic succession of the Ouchbis Formation (*Oxynoticeras oxynotum – Pleuroceras spinatum* zones, Upper Sinemurian – Pliensbachian). In the Foum Tillicht section, a stratigraphic interval comparable to the lower member at Foum Zidet is directly overlain by thick sponge-microbial mounds (Neuweiler et al., 2001). The lower member of the Foum Zidet Formation at Foum Zidet consists of several facies types that differ chiefly in their degree of storm-reworking and in the abundance and taphonomic preservation of biotic components. The lower member of the Foum Zidet Formation is subdivided here into six depositional units that differ in the proportion of the particular facies types. They include microbialite-dominated unit 1, sponge-dominated units 2 and 3, bioclast-dominated units 4 and 5, and microbialite-dominated unit 6.

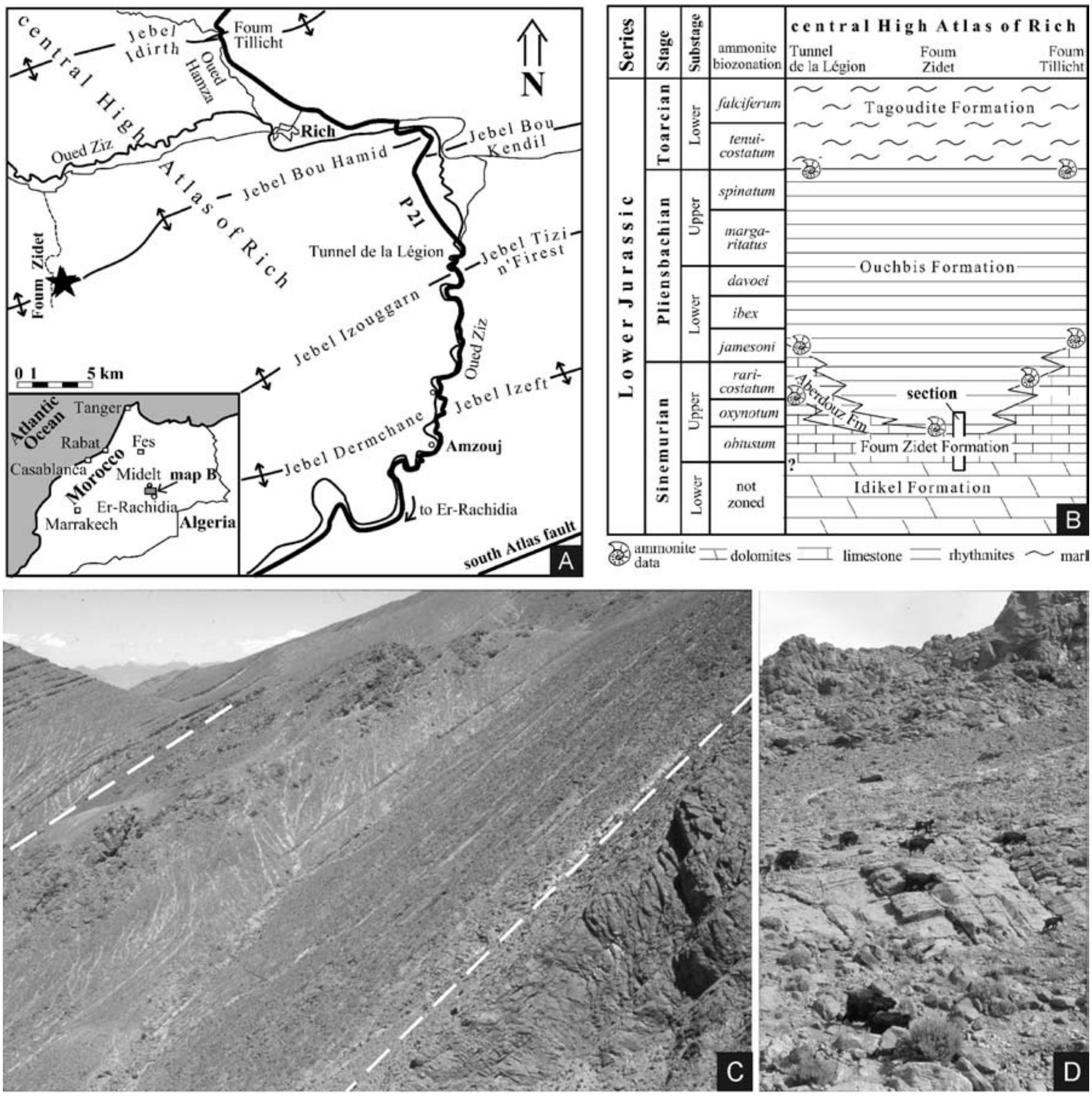


Figure 1 – A. Schematic map of the Rich area with position of the Foum Zidet section (asterisk). B. Spatial and temporal relationship of the Foum Zidet Formation to other Lower Jurassic deposits in the Central High Atlas and the stratigraphic position of the Foum Zidet section (Fig. 1C). C. Section at Foum Zidet, with the Idikel Formation at the base, the Foum Zidet Formation with large-scale sponge-microbialite mounds, and the Ouchbis Formation in the upper part. White lines mark the lower and upper boundary of the Foum Zidet Formation. D. The upper part of the lower member formed by oncoidal floatstones is overlain by a poorly exposed middle member, which is replaced by the sponge-microbial mounds of the upper member of the Foum Zidet Formation.

Facies types and their spatial distribution

Results. Six facies types were discriminated with a Q-mode cluster analysis of 31 samples using the group-average linking method and Bray-Curtis similarity (Fig. 2). The analysis is based on the volumetric abundances of 11 components, including chaetetids, siliceous sponges, brachiopods, bivalves, gastropods, crinoids, serpulids, bryozoans, *Terebella*, peloids and microbial crusts. The facies thus chiefly differ in abundance of the components (Fig. 3) but they have also some consistent similarities in sedimentologic features related to their fabric, geometry and internal structure. Micro-encrusters represented by *Radiomura, Terebella* and nubeculariids/*Tubiphytes* were mostly embedded within microbial crusts and their abundances were thus not included into this analysis.

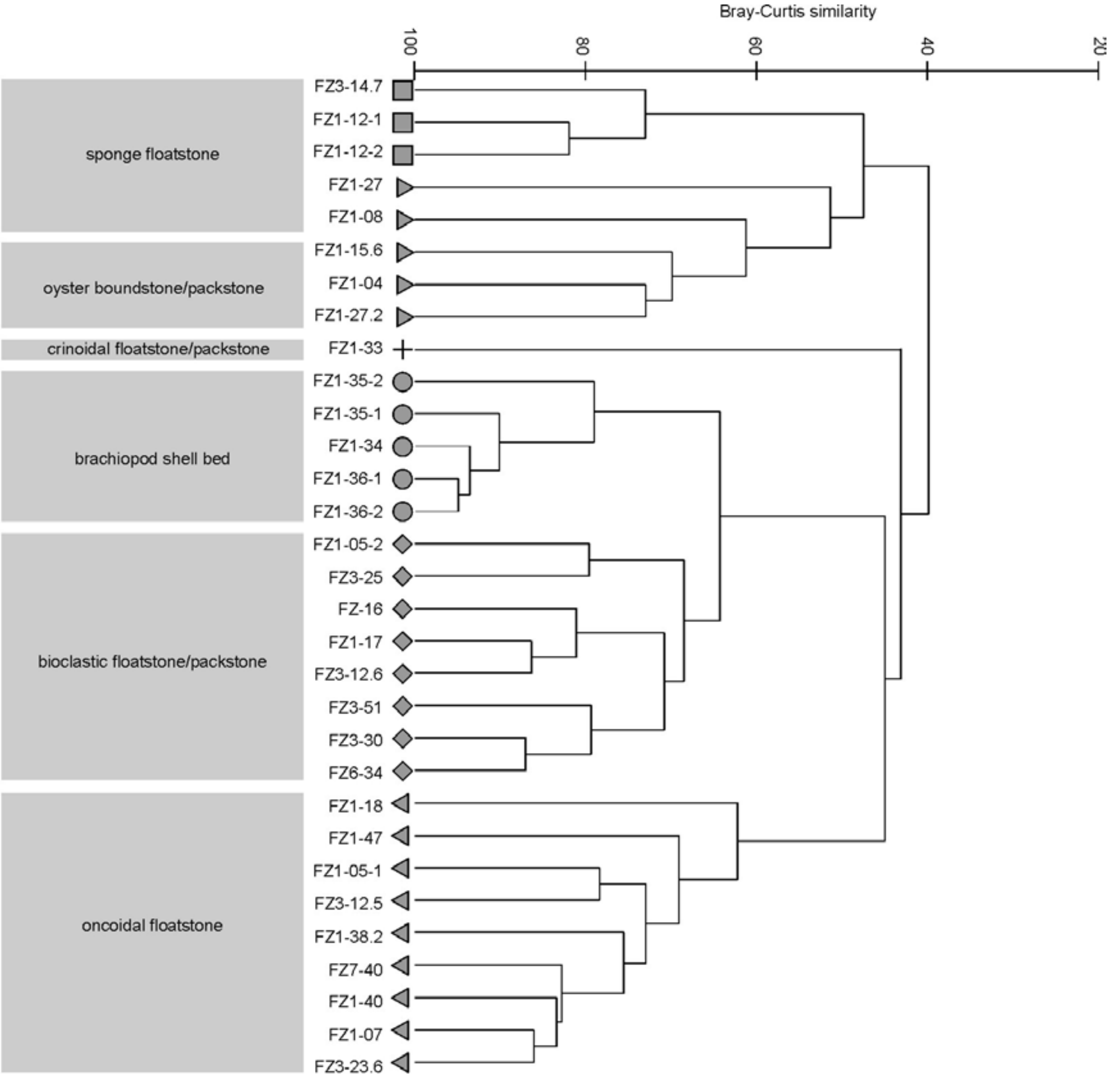


Figure 2 – Q-mode cluster analysis performed with the group-average linking method and Bray-Curtis similarity and based on the volumetric abundances of 11 components (chaetetids, siliceous sponges, brachiopods, bivalves, gastropods, crinoids, serpulids, bryozoans, *Terebella*, peloids, and microbial crusts).

(1) Sponge floatstones form 50-100 cm thick micrite-rich beds that are dominated by hexactinellid sponges, which are dispersed or loosely packed and rarely form a framework (Fig. 4A-E). They occur mainly in the middle part of the lower member. Sponges do not attain extensive dimension nor dense packing as in sponge-microbial mounds in the upper part of the Foum Zidet Formation (Neuweiler et al., 2001). They are mostly several centimeters to decimeters in size and characterized by conical and cylindrical shapes (Fig. 4A-B). Sponges typically exhibit high proportions of encrusting serpulids and bivalves; encrusting bryozoans are less common. External microbial crusts are thin and rare, although internal sponges cavities are commonly filled with microbial micrite. Massive or branching chaetetid sponges are common (Fig. 4D). The micritic sediment between sponges contains dispersed or loosely-packed debris or complete shells of brachiopods, bivalves, gastropods, and crinoid ossicles. In some cases, the cementing bivalve

Nanogyra forms 1 cm-thick, in situ preserved, flat aggregates that are directly cemented to the top of large sponges. The spatial distribution of dispersed or loose sponges and associated brachiopods and *Nanogyra* in cross-sections and plane-views is characterized by clumps that reach 10-50 cm in size and are separated by wackestones with dispersed bioclasts (Fig. 4C). Aggregates of rhynchonellids and terebratulids are commonly associated with sponge clumps (Fig. 4E). The clumps themselves appear to be randomly distributed.

(2) Oncoidal floatstones form 20-50 cm-thick, poorly sorted beds with dispersed-loosely packed and randomly oriented bioclasts (Fig. 5A-B). They are present mainly in the lower and upper parts of the lower member and are dominated by microbial crusts that asymmetrically coat hexactinellid sponges, brachiopod valves, complete brachiopod shells or other bioclasts. The oncoids are commonly coalescing with their microbial neighbors and may form a microbialitic framework (i.e., the deposits can be termed also as oncoidal boundstones). Mesoscopically, the microbial crusts are structurless or finely laminated. Microscopically, they are mainly formed by laminae of dense micrite and less commonly by peloidal micrite. The laminae are mostly iron stained. Encrusters are mainly represented by bryozoans, nubeculariids (including *Tubiphytes* with thin outer layer) and *Radiomura*. *Terebella* is restricted to intra-shell cavities. Multiple alternations of thin microbial crusts with bryozoans are a typical feature of this facies type. *Aka* borings are common. In addition to microbial crusts, degraded siliceous sponges and brachiopods prevail. Bivalves, chaetetids, crinoid ossicles and gastropods are less common. In contrast to the presence of clumps in the sponge floatstones, spatial distribution of sponges, brachiopods and bivalves is more or less random in oncoidal floatstones.

(3) Oyster facies are represented by thin boundstone pavements or 10-20 cm thick packstones. They occur mainly in the middle part of the lower member and rarely in its lower and upper parts. Packstones are loosely-densely packed, moderately sorted and may show internal stratification with erosional boundaries. Boundstones are mainly represented by thin aggregates of *Nanogyra nana* attached to siliceous sponges or chaetetids (Fig. 4F). Microbial crusts are uncommon, restricted to internal sponge cavities and pores, and encrusters are mainly represented by serpulids and bryozoans. Brachiopods, crinoids and gastropods are relatively rare. The micrite-rich matrix contains abundant peloids.

(4) Bioclastic floatstones/packstones are loosely or loosely to densely packed, poorly to moderately sorted and locally show small-scale internal stratification consisting of cm-scale layers with varying packing density and sorting, size grading and internal erosional boundaries (Fig. 5D-F). They are most common in the middle and upper parts of the lower member. Densely packed beds are characterized by good to moderate sorting and preferred orientation of stacked or nested disarticulated valves. They are dominated by fragmented and disarticulated brachiopod debris and fragments of siliceous sponges that float in the peloidal-rich micritic matrix. Bioclasts are frequently encrusted by bryozoans and serpulids and coated by thin microbial crusts. Bivalves and crinoids are less common.

(5) A brachiopod shell bed marks a unique, 150 cm-thick stratigraphic interval in the upper part of the lower member that is formed by densely-packed and poorly sorted, articulated brachiopods commonly preserved in their life position (Fig. 5C). Shells are coated with thin microbial crusts and are encrusted by bryozoans. The shell cavities are filled with microbial micrite and the cryptic polychaete *Terebella*. Non-rigid siliceous sponges and juvenile hexactinellids, bivalves and crinoids are dispersed in a micritic, peloidal-rich matrix among brachiopod shells.

(6) Crinoidal floatstones/packstones occur in the upper part of the lower member and are represented by loosely/densely packed and moderately sorted beds with concordantly oriented stem segments of crinoids, dispersed debris of brachiopods, bivalves and siliceous sponges in a peloidal-rich micritic matrix. Thin microbial crusts are common. Encrusters are mainly represented by bryozoans; serpulids are less common. This facies type is laterally replaced by bioclastic floatstones and packstones.

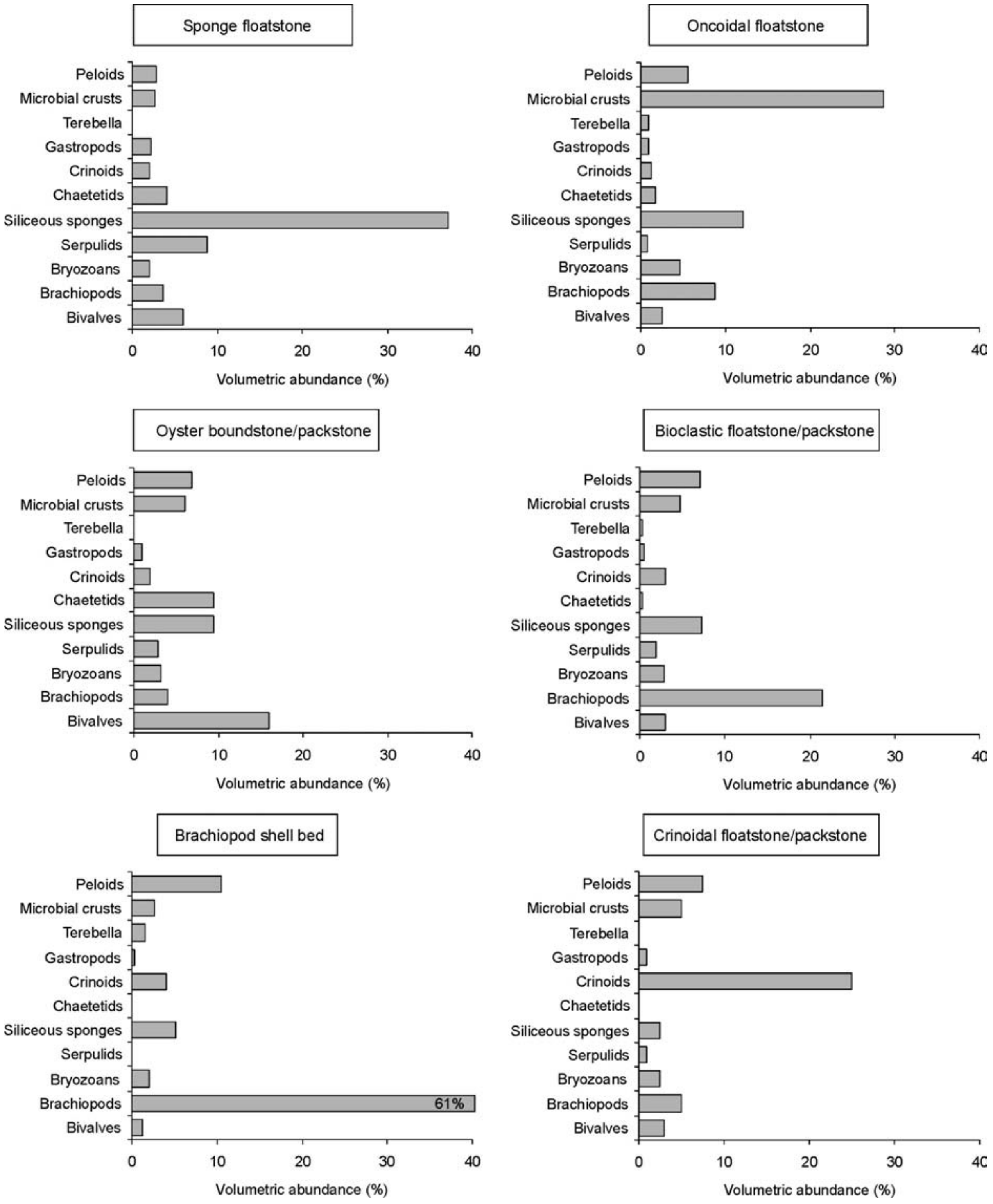


Figure 3 – Volumetric abundances of the ten most common components in six facies types of the lower member of the Foum Zidet Formation.

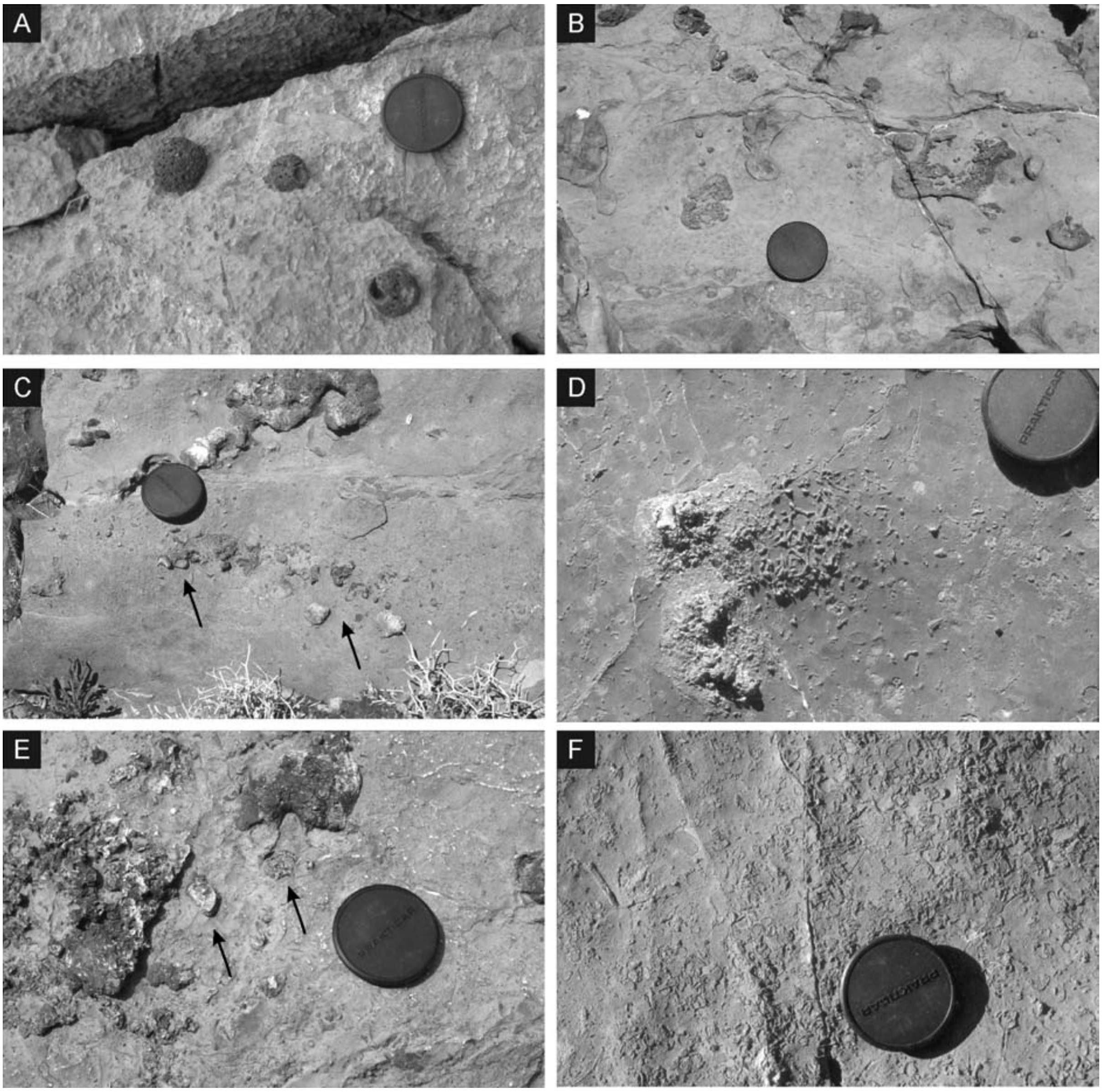


Figure 4 – Sponge floatstones (A-E) and oyster boundstone (F) of the lower member of the Foum Zidet Formation. A. Bedding plane view of dispersed hexactinellid sponges. B. Bedding plane view of degraded siliceous sponges. C. Cross-section view of siliceous sponges with brachiopod clumps (black arrows). D. Bedding plane view of branched chaetetid sponge. E. Bedding plane view of siliceous sponge with terebratulid brachiopods (black arrows). F. Bedding plane view of oyster boundstone formed by thin pavement with *Nanogyra nana*.

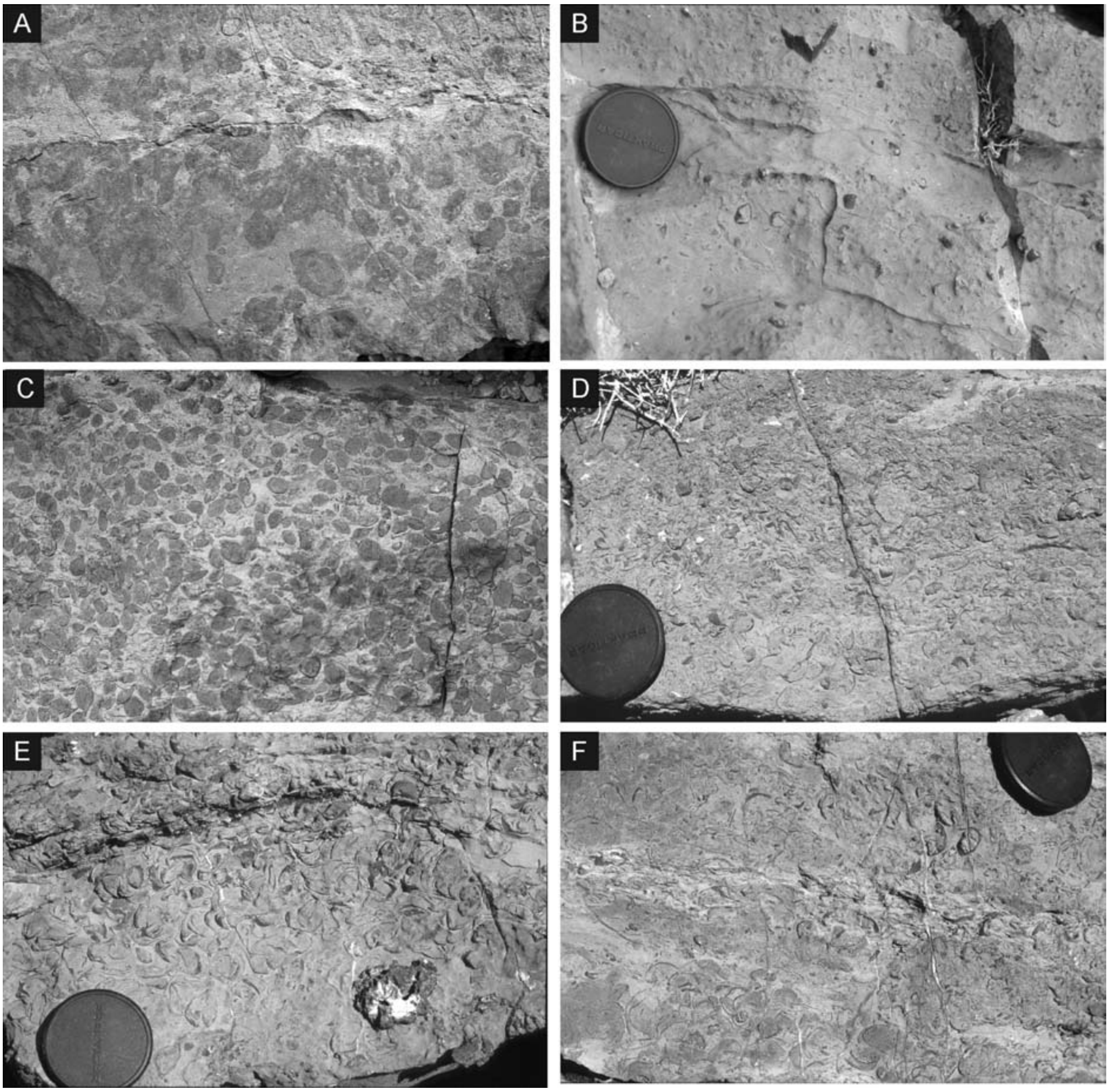


Figure 5 – Oncoidal floatstones (A-B), bioclastic floatstones/packstones (C-E), and the brachiopod shell bed (F) of the lower member of the Foum Zidet Formation. A. Cross-section view of oncoidal floatstone. B. Dispersed brachiopods in oncoidal floatstone. F. The brachiopod shell bed in cross-section view. D. Cross-section view of bioclastic packstone with brachiopods and bivalves. E. Cross-section view of bioclastic packstone with nested and stacked brachiopods and dispersed sponge fragments. F. Small-scale alternation of bioclastic packstones and floatstones with distinct packing and sorting in cross-section view.

Discussion. Biofabric, geometry, and internal structure of the facies types enable to interpret their position along an environmental gradient. Although the main source of the variation between facies types are varying amounts of sponges, microbialites, bivalves and brachiopods, the assignment of the facies types to environments is not based on volumetric abundance of biotic components. Internal stratification consisting of cm-scale alternation of deposits with distinct packing and sorting, internal erosional surfaces, preferred stacked, edgewise and nested orientation of bioclasts, and concave-up valves indicate episodic wave activity (Middleton, 1967; Futterer, 1982; Salazar-Jiménez et al., 1982) above normal storm wave base (NSWB). The micrite-rich matrix and the lack of amalgamation indicate that reworking was episodic and low-energy conditions prevailed during background conditions. Densely-packed bioclastic, oyster and crinoidal packstones with these features are assigned to environments with bioclastic-rich substrates above NSWB.

Loosely packed and poorly to moderately sorted bioclastic floatstones, oyster boundstones and some sponge and oncoidal floatstones with randomly oriented bioclasts and signs of bioturbation were deposited in environments with lower storm intensity and frequency than packstones with similar biotic composition. High proportions of disarticulated and fragmented shell debris, thin layers with well sorted and densely packed bioclasts, oncoids and rare intraclasts and shells filled with sparite may indicate short-term episodic reworking coupled with winnowing or rapid burial. Therefore, facies with such features probably originated in environments below NSWB and above maximum storm wave base (MSWB).

Poorly sorted and loosely packed sponge floatstones with patchy shell aggregates and rare microbial crusts, and oncoidal floatstones with brachiopods and bivalves embedded in microbial framework with absence of erosion or amalgamation indicate undisturbed environments below MSWB. Similarly, the brachiopod shell bed with in situ preserved concentrations of terebratulids originated in low-energy environments undisturbed by storm reworking. Their spatial replacement with thin layers enriched with crinoid and bioclastic debris (i.e., crinoidal and bioclastic floatstones/packstones) hints at environments in the immediate proximity MSWB.

The sedimentologic subdivision of the facies types into the three environments is based on features that are related to episodic high-energy events. Background times, however, were probably consistently characterized by low-energy conditions. This indicates that the environmental transect represented by the deposits at Foum Zidet reflects rather uniform environments that differed chiefly in intensity of storm-reworking and winnowing as well as abundances of the main biotic groups. Bathymetric distribution of reef-forming organisms differed from that typical of other Jurassic reef habitats (Leinfelder et al., 1994; Leinfelder, 2001). On one hand, sponge-dominated communities extended into very shallow environments of Central High Atlas Basin. On the other hand, coral or coral-sponge communities did not occur in the shallowest environments of Central High Atlas Basin. The environments above normal storm wave base were inhabited by corals and encrusters of the *Bacinella*-*Lithocodium* community both in Late Triassic and in Late Jurassic environments (e.g., *Lithocodium, Thaumatoporella*, *Bacinella* or *Cayeuxia,* Leinfelder et al., 1993; Schmid, 1996; Dupraz and Strasser, 1999). The absence of light-dependent encrusters and algae and the presence of *Tubiphytes* with small tests and a very thin micropeloidal outer layer (Schmid, 1996) in facies affected by storm-reworking indicates that the lower boundary of the photic zone was very shallow during deposition of the lower member of the Foum Zidet Formation. Dasycladacean algae were found in intraclastic and bioclastic packstones and grainstones in the Foum Tillicht section in the stratigraphic levels comparable to the lower member of the Foum Zidet Formation (lower mound interval, Neuweiler et al., 2001). The absence of corals and light-dependent encrusters may be due to environmental conditions related to oceanographic or climatic events that did not allow their settlement and recruitment and favored formation of ramps rather than reefs (Burchette and Wright, 1992) and/or due to the effect of slow recovery of phototrophic carbonate producers after the end-Triassic mass extinction (Wilmsen, pers. comm.). The facies types probably reflect deposition on a low-angle slope without a site-specific peak in carbonate production, indicating that the biostromes formed on a slightly inclined, homoclinal ramp in environments above and below maximum storm wave base. Preferential occurrence of large-scale sponge-microbialite mounds at the upturned, foot wall edges of fault blocks that formed during the initial rifting (Evans and Kendall 1977; Milhi et al.

2002) indicates that the direction of the ramp inclination may have been driven by fault-controlled topography of the Rich block.

Temporal distribution of facies types and components

Results. At the base of the lower member (Fig. 6), a 5-6 m thick interval (microbialite-dominated unit 1) consists of oncoidal floatstones that originated below MSWB. They contain predominantly microbial crusts (17%) that coat sponges (10%), brachiopods (8%) and bivalves (7%). Chaetetids are rare (< 1%). The middle part of the lower member is formed by two, about 10 and 15 meters thick intervals dominated by sponge floatstones with hexactinellid sponges (sponge-dominated units 2 and 3), locally with bioclastic floatstones and packstones rich in brachiopods (7-20%), oysters (5-6%) and chaetetids (3%). Abundant encrusting serpulids (3-6%) and bryozoans (3-3.5%) and bivalve and sponge borings are associated with hexactinellid sponges (14-23%) and microbial crusts (5-8%). Brachiopods and bivalves are common. The facies types represent environments ranging from above NSWB up to below MSWB. In contrast to the upper member of the Foum Zidet Formation with meter-scale mounds, the sponge and microbial limestones in the lower member form sheet-like beds that rarely increase in thickness on the scale of several centimeters. These intervals are separated by about 50 cm-thick bundles of bioclastic beds with abundant brachiopod debris. Several bioclastic-rich intervals occur at similar stratigraphic positions and can be thus correlated between the two sections. However, some bioclastic floatstones and packstones occur also within the sponge intervals and are spatially restricted to one section only (e.g., in the middle part of sponge-dominated unit 2).

The upper part of the lower member (units 4-6) is dominated by bioclastic floatstones and packstones and oncoidal floatstones with abundant brachiopods and bivalves (Fig. 6). The oncoidal and bioclastic-rich limestones form groups of beds that can be correlated between the two sections. In bioclast-dominated unit 4 brachiopods (10%), bivalves (8%) and microbial crusts (8%) prevail, followed by chaetetids (7%) and sponges (6%). Crinoids substantially increase in abundance (6%) and serpulids are rare (< 1%) in comparison to the underlying units. Encrusters are mainly represented by bryozoans (3%) and nubeculariid foraminifers (2%). This unit is dominated by facies that originated above and below NSWB.

Within the upper part of the lower member, about 50 m above the base of the Foum Zidet Formation, a 150 cm thick brachiopod shell bed (unit 5) consisting of densely packed articulated shells (more than 50%) occurs in both sections (Fig. 6). Siliceous sponges (5%) and crinoids (5%) are less common. This bed can be traced for about one kilometer in a westward direction. The encrusters are represented by bryozoans (2%). Microbialite-dominated unit 6 in the uppermost part of the lower member consists of oncoidal floatstones that locally alternate with crinoidal and bioclastic floatstones. It contains mainly microbial crusts (30%), followed by common brachiopods (12%), hexactinellid sponges (11%) and bryozoans (6%). Chaetetids (3%), crinoids (3%), and bivalves (2%) are less common. The unit is dominated by facies that originated below NSWB and MSWB.

The units significantly differ in their abundance of components (Tab. 1, one-way ANOSIM, R = 0.183, p = 0.01). As follows from pairwise comparisons, microbialite-dominated units 1 and 6 do not differ in their composition, but there are high or borderline differences between sponge-dominated units 2-3, bioclast-dominated units 4-5 and microbialite-dominated unit 6.

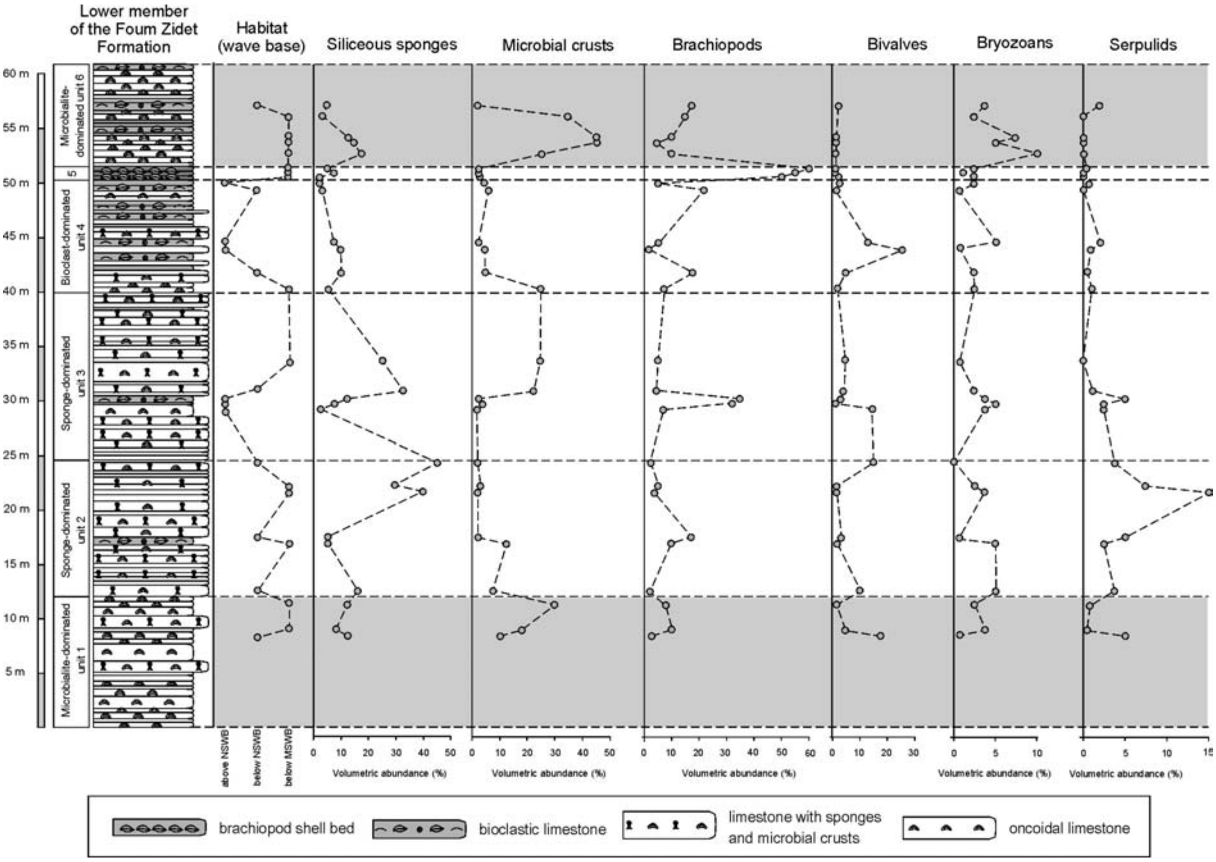


Figure 6 – Simplified section of the lower member of the Foum Zidet Formation with the subdivision into six depositional units and relative abundances of the main biotic groups.

One-way ANOSIM (temporal effects on components)	R	p-value (alpha = 0.05/6)	Number of permutations	Number of permuted R≥observed R
Global test	0.183	0.01	10000	103
Pairwise tests:				
microbialite unit 1 vs. sponge units 2-3	-0.012	0.479	1001	479
microbialite unit 1 vs. bioclast units 4-5	0.214	0.090	1820	164
microbialite unit vs. microbialite unit 6	-0.069	0.683	126	86
sponge units 2-3 vs. bioclast units 4-5	0.214	0.014	10000	137
sponge units 2-3 vs. microbialite unit 6	0.259	0.033	3003	99
bioclast units 4-5 vs. microbialite unit 6	0.238	0.050	6188	309

Table 1 - Results of one-way analysis of similarities showing between-unit differences in abundances of components.

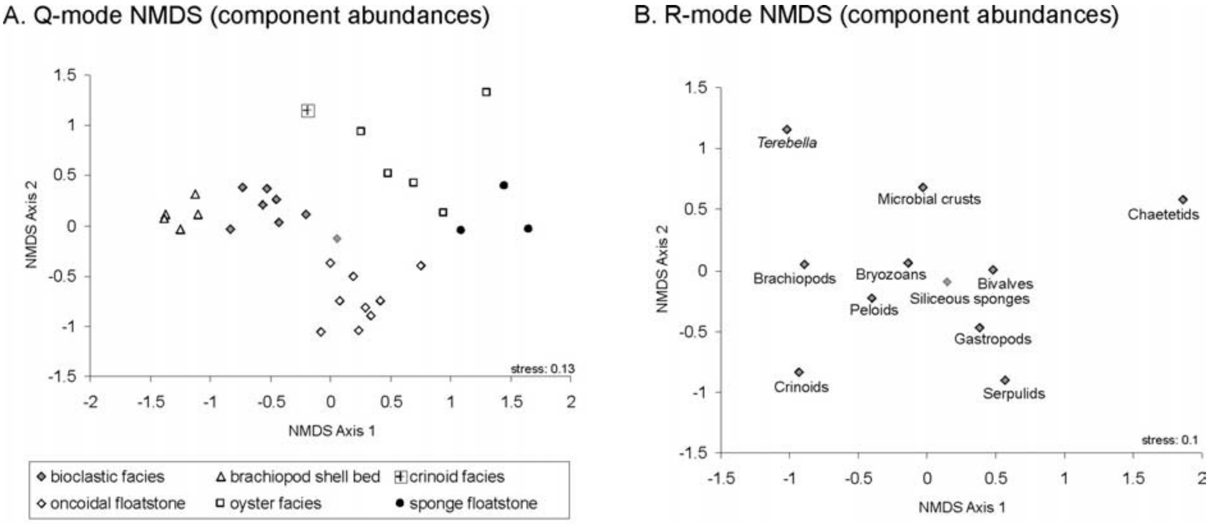
Discussion. Each depositional unit is dominated by particular deposit types that indicate an average level of wave base during its deposition. This makes it possible to interpret temporal trends in depositional conditions related to the level of storm wave-base and/or water depth (Fig. 6). Microbialite-dominated units 1 and 6 in the lowermost and uppermost part of the member are dominated by low-energy facies types that originated below NSWB and MSWB. In contrast, sponge-dominated units 2 and 3 from the middle part of the member contain facies types that record the complete bathymetric transect from above NSWB up to below MSWB. Bioclastic floatstones and packstones in bioclast-dominated unit 4 reflect a peak in storm intensity and frequency in the lower member, indicating a lowering of normal storm wave-base or a decrease in relative sea level. The brachiopod shell bed marks the transition between the bioclast-dominated unit 4 and microbialite-dominated unit 6 and probably reflects a decrease in storm activity. In summary, the lower member of the Foum Zidet Formation records the change from low-energy conditions with restricted water mixing below storm wave base in the lower part to medium-energy conditions in the middle part with a peak in storm activity during the bioclast-dominated unit 4. A final reversal to low-energy conditions with restricted circulation is recorded in the upper part of the lower member. The lower member was thus affected by long-term variations in storm intensity and frequency that can be related to changes in level of wave base or water depth. Such variations might have caused concomitant changes in the circulation regime, background current regime, and oxygen concentrations near the sea-floor.

Abundance and spatial distribution of components

Q-mode analyses. Q-mode NMDS based on the components indicates that sponge floatstones and oyster boundstones/packstones are more similar in composition compared to other facies types (Fig. 7A). In addition, oyster boundstones/packstones are more similar in composition to bioclastic floatstones/packstone than to oncoidal floatstones and the brachiopod shell bed. Oncoidal floatstones are compositionally similar to sponge floatstones and bioclastic floatstones/packstones. The brachiopod shell bed is more similar in composition to bioclastic floatstones/packstones than to other facies types. In general, this pattern can be described as a compositional replacement of oyster boundstones/packstones and sponge floatstones by bioclastic and oncoidal facies and, finally, by the brachiopod shell bed (Fig. 7A).

R-mode analyses. Bivalves, gastropods and serpulids group together in the R-mode cluster analysis. The second group is formed by siliceous sponges, microbial crusts, and bryozoans and the third group consists of brachiopods and peloids. This pattern in abundance similarity among the components is relatively comparable to that based on the Q-mode analysis, with brachiopods and bivalves occupying opposite parts of the compositional gradient. R-mode NMDS based on the components indicates that the main rock-forming components show a relatively ordered pattern in their abundance, with chaetetid sponges being relatively dissimilar from all other components (Fig. 7B). They co-occur mainly with bivalves (BC = 31.5) and siliceous sponges (BC = 31). Crinoids and *Terebella* are also rather dissimilar in their abundances from other components, although both share similarities with brachiopods. Siliceous sponges have similar abundance patterns as bryozoans (BC = 63.4), serpulids (BC = 56.8), bivalves (BC = 55), gastropods (BC = 51.6), and brachiopods (BC = 44.9). Abundance of microbial crusts is similar to that of bryozoans (BC = 61.4) and siliceous sponges (BC = 54.1). Brachiopods are similar in their abundance patterns to *Terebella* (BC = 63.6), bryozoans (BC = 52.7), crinoids (BC = 46.9) and siliceous sponges (BC = 44.9).

Environmental differences. There are very low and insignificant differences in the component abundances among the three environments (one-way ANOSIM, R = 0.097, p = 0.086). When the environments above MSWB are compared with the environments below MSWB, the difference is low but significant (R = 0.13, p = 0.016). Microbial crusts increase and bivalves decrease in their abundance towards the deeper environments (Fig. 7C). The differential distribution of bivalves and microbial crusts is supported by differences among environments in terms of 95% bootstrapped confidence intervals (Fig. 7C). Hexactinellid sponges reach their abundance peak in environments below NSWB and above MSWB, and brachiopods are most common in environments below MSWB. However, both groups show large overlaps among environments in terms of 95% bootstrapped confidence intervals.



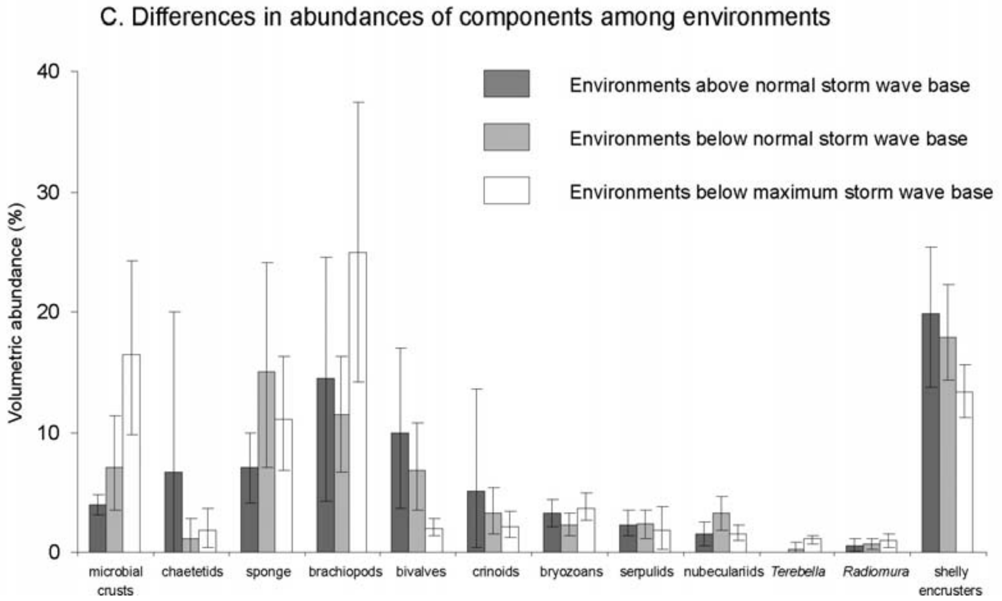


Figure 7 - Compositional relationship between samples, components and encrusters. A. Q-mode non-metric multidimensional scaling (NMDS) of 31 samples based on the volumetric abundances of 11 components. It shows compositional similarities among the six facies types. B. R-mode NMDS of 11 components based on their volumetric abundances. C. Differences among environments in mean abundance of components with 95% bootstrapped confidence intervals. Note that the abundance of bivalves increases and abundance of microbial crusts decreases toward the shallow environments.

One-way ANOSIM (substrate effects on encrusters)	R	p-value (alpha = 0.05/6)	Number of permutations	Number of permuted R≥observed R
Global test	0.514	<0.0001	10000	0
Pairwise tests:				
sponges vs. microbial crusts	0.785	0.0001	10000	1
sponges vs. bioclastic debris	0.331	0.0139	5005	70
sponges vs. brachiopod shells	0.813	0.0021	462	1
microbial crusts vs. bioclastic debris	0.256	0.0011	10000	11
microbial crusts vs. brachiopod shells	0.507	0.0009	4368	4
bioclastic debris vs. brachiopod shells	0.663	0.0005	2002	1

Table 2 – Results of one-way analysis of similarities showing between-substrate differences in abundances of encrusters.

Abundance and spatial distribution of encrusters

Q-mode analyses. Q-mode cluster analysis of 31 samples based on the abundances of bivalves (predominantly represented by the cementing *Nanogyra nana*), bryozoans, serpulids, nubeculariids (including *Tubiphytes* with thin outer layer), *Terebella, Radiomura* and juvenile siliceous sponges is used for discrimination of six groups of samples representing distinct encruster communities at a Bray-Curtis similarity of 60 (Fig. 8A). Hexactinellids and chaetetids are not used in multivariate analyses (with exception of juveniles) because they define one of the substrate types. Q-mode NMDS based on the abundance of encrusters shows six groups of samples with distinct encruster abundances (Fig. 8B). These groups are comparable to encrusting communities described from other Jurassic environments time intervals (Schmid, 1996; Dupraz and Strasser, 1999, 2002; Olivier et al., 2004a; Reolid et al., 2005). The compositional relationship of the six sample groups visible in Q-mode NMDS indicates no discrete boundaries between the encruster communities. In general, bivalve- and serpulid-dominated sample groups are replaced by diverse bryozoan-serpulid-bivalve sample groups and finally by bryozoan-dominated sample groups with *Terebella* and nubeculariids. The first group, dominated by serpulids (about 10%) is represented by two samples of sponge floatstones. Bryozoans and bivalves are also common (2-3%), *Radiomura* is rare (< 1%). The second group of six samples, dominated by *Nanogyra* (about 16%) and serpulids (3%), is typical of oyster boundstones/packstones and sponge floatstones. Bryozoans, nubeculariid foraminifers and juvenile siliceous sponges are less common (< 3%). The third, bivalve-bryozoan group is represented by six samples of oncoidal and bioclastic floatstones with bivalves (4%), bryozoans (3%), juvenile sponges (2%), and rare nubeculariids and *Radiomura* (< 2%). The fourth group formed by eight samples of bioclastic and crinoidal floatstones is characterized by relatively high evenness, with brozoans, nubeculariids, bivalves and serpulids occurring in similar abundances (2-3%). The fifth group with four samples is dominated by bryozoans (6%) and nubeculariids (5%), and is mainly represented by oncoidal floatstones. Juvenile sponges, *Radiomura*, bivalves, and *Terebella* are less common (< 2%). The sixth group is mainly restricted to the brachiopod shell bed that is dominated by bryozoans (about 2%), *Terebella* (1.75%), and juvenile siliceous sponges (1.5%).

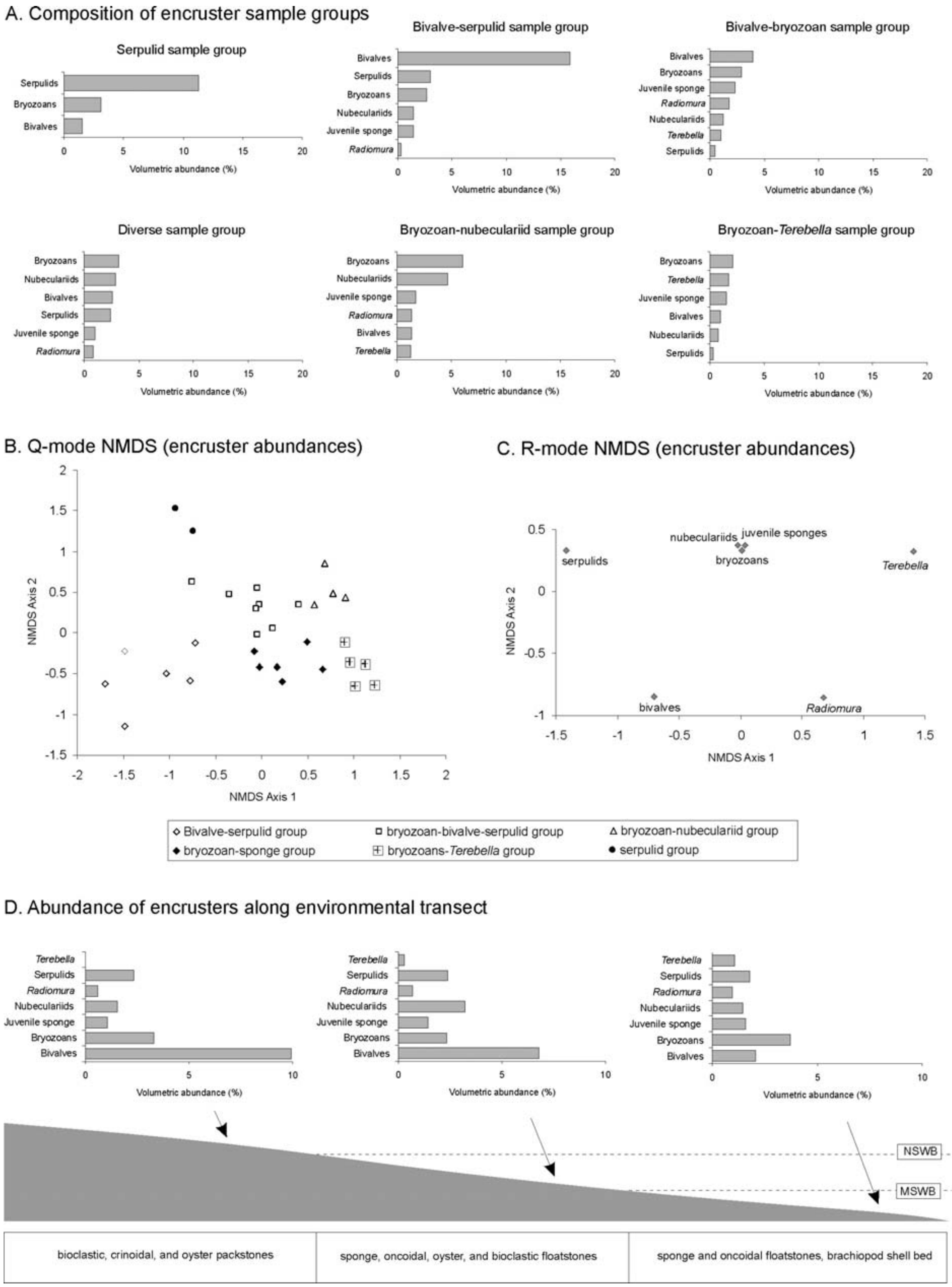


Figure 8 – A. Volumetric abundances of the encrusters in six sample groups, which were defined on the basis of a Q-mode cluster analysis based on the abundances of encrusters.
B. Q-mode NMDS of 31 samples based on the volumetric abundances of seven encrusters. It shows compositional similarities among the six encruster sample groups. C. R-mode NMDS of seven encrusters based on their volumetric abundances. D. Variations in encruster abundances along an environmental transect in the lower member of the Foum Zidet Formation. Note that bivalves dominated in the shallow and bryozoans in the deep environments.

R-mode analyses. Using R-mode cluster analysis, two groups of encrusters can be discriminated: a first group formed by bivalves, serpulids, and gastropods, and a second group with bryozoans, nubeculariids, juvenile sponges, *Radiomura*, and *Terebella*. R-mode NMDS demonstrates a close similarity in the abundance patterns of nubeculariids, bryozoans and juvenile sponges (Fig. 8C). Although all encrusters can co-occur, their abundances vary to some predictable degree. Thus serpulids and bivalves, sharing similar abundance patterns, are in general replaced by nubeculariids, bryozoans and juvenile sponges, which may be replaced by *Terebella* or *Radiomura*, in accord with the Q-mode analyses.

Environmental differences. There are low but significant differences in the encruster abundances among the three environments (one-way ANOSIM, $R = 0.196$, $p = 0.01$). The main difference is between the environments above MSWB on one hand and the environments below MSWB on the other ($R = 0.257$, $p < 0.0001$). The poor difference among environments is mainly caused by presence of several sample groups in more than one environment. For example, both serpulid- and bryozoan-dominated sample groups occur in environments below MSWB. In addition to the decrease in the abundance of bivalves, *Terebella* increases in abundance towards the deeper environments (Fig. 8D). In terms of 95% bootstrapped confidence intervals, serpulids, bryozoans, *Radiomura* and juvenile sponges do not substantially vary in their abundance among environments (Fig. 8D).

Substrate preferences. The overall abundance of shelly encrusters is significantly higher on sponge substrates than on microbial crusts. Sponges are encrusted mainly by bivalves (12%, Fig. 9B) and serpulids (6%, Fig. 9A), followed by less common bryozoans (2%) and nubeculariids (1%). Bioclastic debris was colonized mainly by bivalves (5%), nubeculariids (3%), bryozoans (3%), and less commonly serpulids (2%, Fig. 9C)). Microbial crusts (Fig. 9E) are encrusted by bryozoans (4%, Fig. 9D, F), bivalves (3%) and nubeculariids (2%, Fig. 10B). Juvenile sponges, *Radiomura* (Fig. 10A), *Terebella* and serpulids are less common. Brachiopod shells show the lowest abundance of encrusters in general, consisting of juvenile sponges (2%, Fig. 10C), bryozoans (2%, Fig. 10D-E), and *Terebella* (1.5%, Fig. 10F), with less common bivalves, nubeculariids, and *Radiomura*.

When the abundance of encrusters is compared among four deposits with distinct substrate types (i.e., sponges, microbial crusts, bioclastic debris and brachiopod shells), the between-substrate differences are relatively high (ANOSIM, $R = 0.52$, $p < 0.0001$). With the exception of the borderline significant difference between sponges and bioclastic debris ($R = 0.33$, $p = 0.014$), all pairwise comparisons show high and significant between-substrate differences in the encruster abundances with the Bonferroni correction (Tab. 2). Bivalves and serpulids are significantly more common on sponge substrates than on microbial crusts (Fig. 11A). Bryozoans, *Terebella*, and *Radiomura* are significantly more common on microbial crusts than on sponge substrates. In terms of 95% bootstrapped confidence intervals, five groups of encrusters show significant differences in their abundances among the substrates (Fig. 11B). Although the majority of brachiopods of the Foum Zidet Formation were attached to the substrate with a pedicle, their abundance on sponges and microbial crusts is of interest because they belonged to the dominant elements in the communities. It follows that brachiopods were significantly more common on microbial crusts (10%) than on sponge substrates (3%).

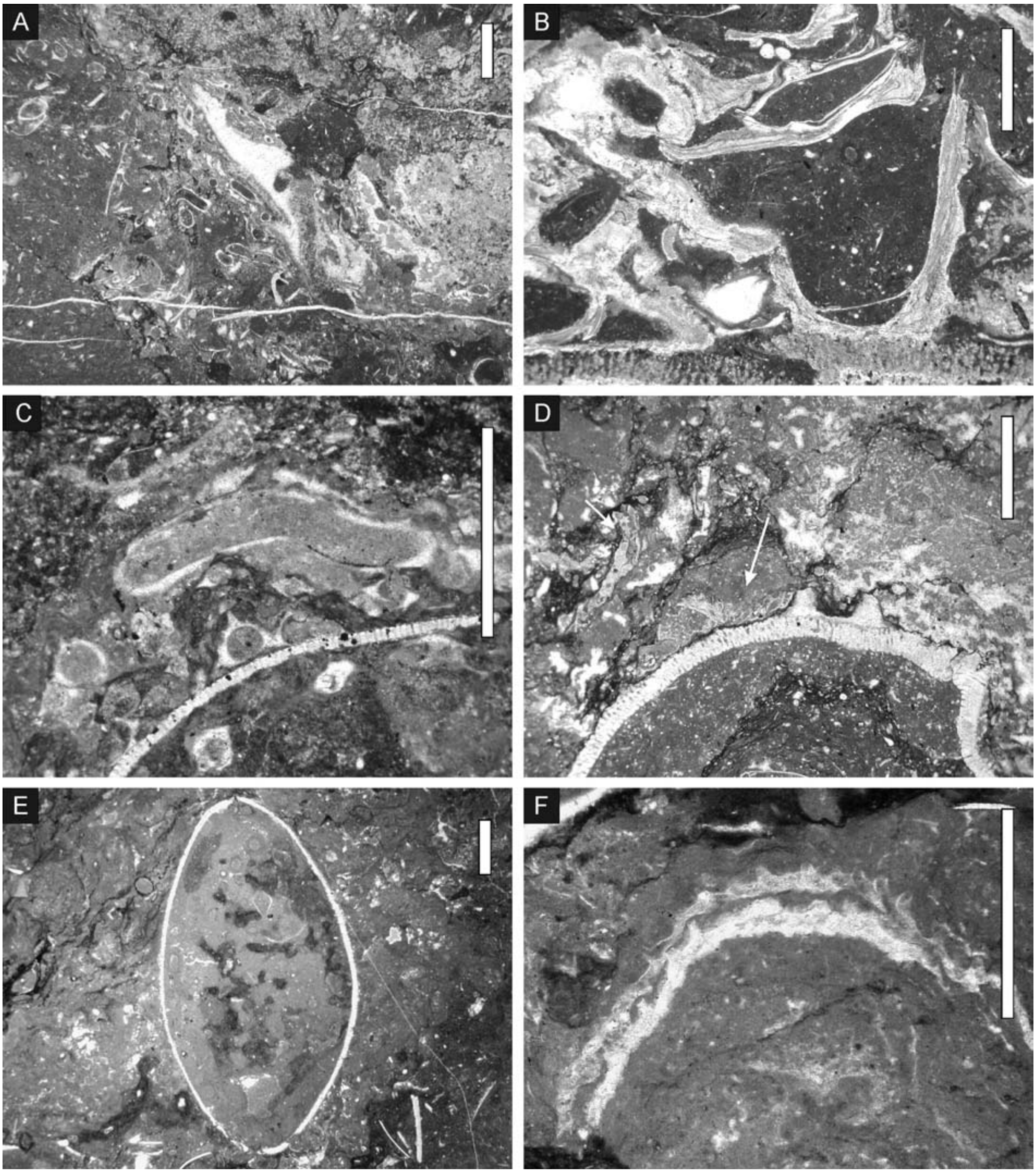


Figure 9 – Encrusters in sponge floatstone (A), oyster boundstone (B), bioclastic floatstone (C) and oncoidal floatstones (D-F). A. Hexactinellid sponge encrusted by serpulids. Note the rarity of microbial crusts. B. Chaetetid sponge encrusted with the cementing oysters *Nanogyra nana*. Microbial crusts are absent. C. Brachiopod fragment encrusted by serpulids. D. Brachiopod shell encrusted by bryozoans (arrows) and coated with microbial crusts. E. Brachiopod shell coated and filled with microbial crusts. F. Sheet-like bryozoans alternating with microbial crusts. Scale bars: 2 mm.

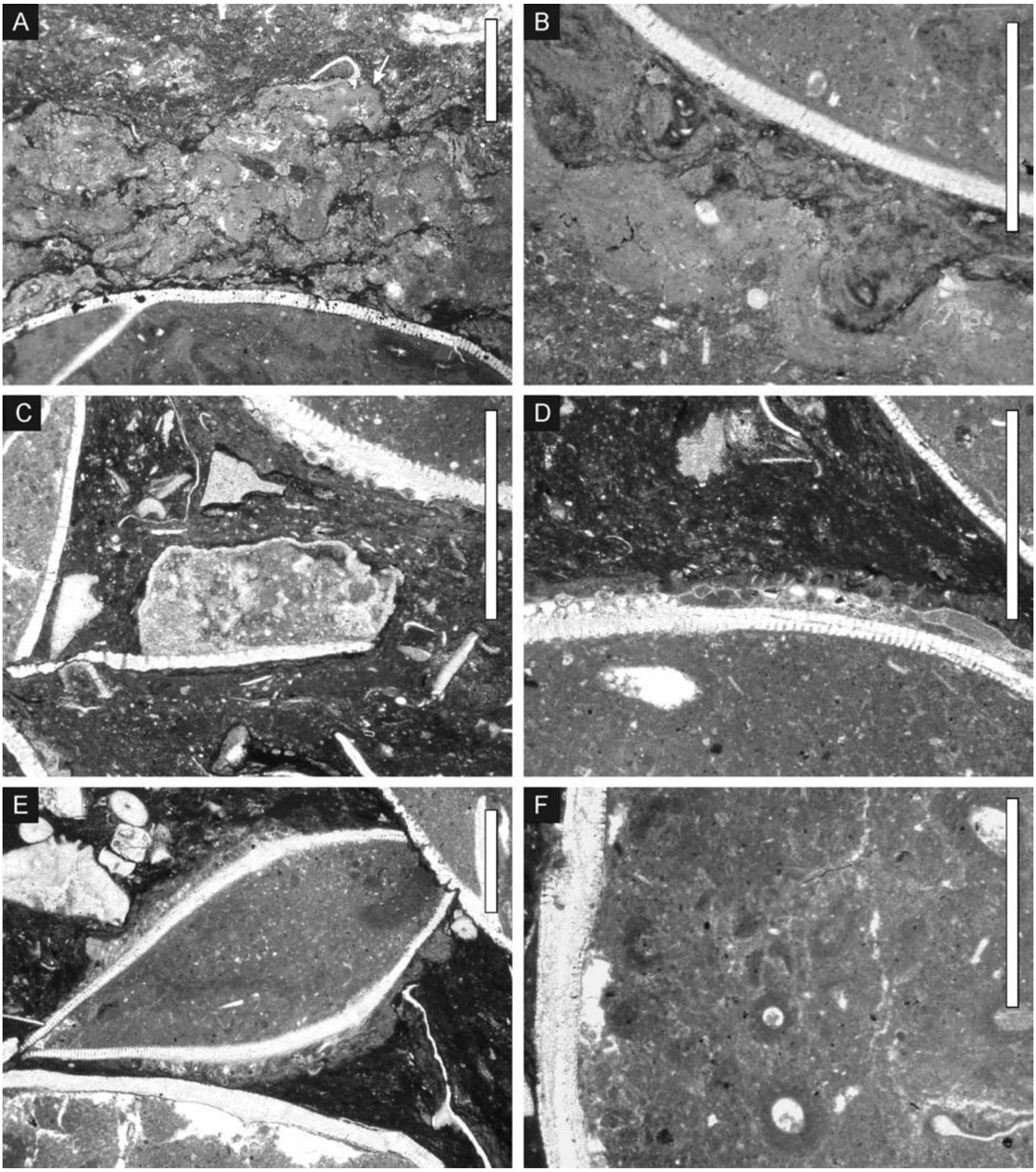


Figure 10 – Encrusters in oncoidal floatstones (A-B) and the brachiopod shell bed (C-F). A. Brachiopod shell coated with microbial crusts with abundant *Radiomura* (arrow). Note the presence of Fe-stained laminae within the microbial crusts. B. Brachiopod shell coated by two distinct microbial crusts. The first crust contains Fe-stained laminae and *Tubiphytes* with a very thin outer layer. C. Juvenile sponge attached to a brachiopod fragment. D. Bryozoans attached to external wall of brachiopod shell. E. Bryozoans attached to both valves of juvenile brachiopod. F. *Terebella* occupying the interior of brachiopod shell. Scale bars: 2 mm.

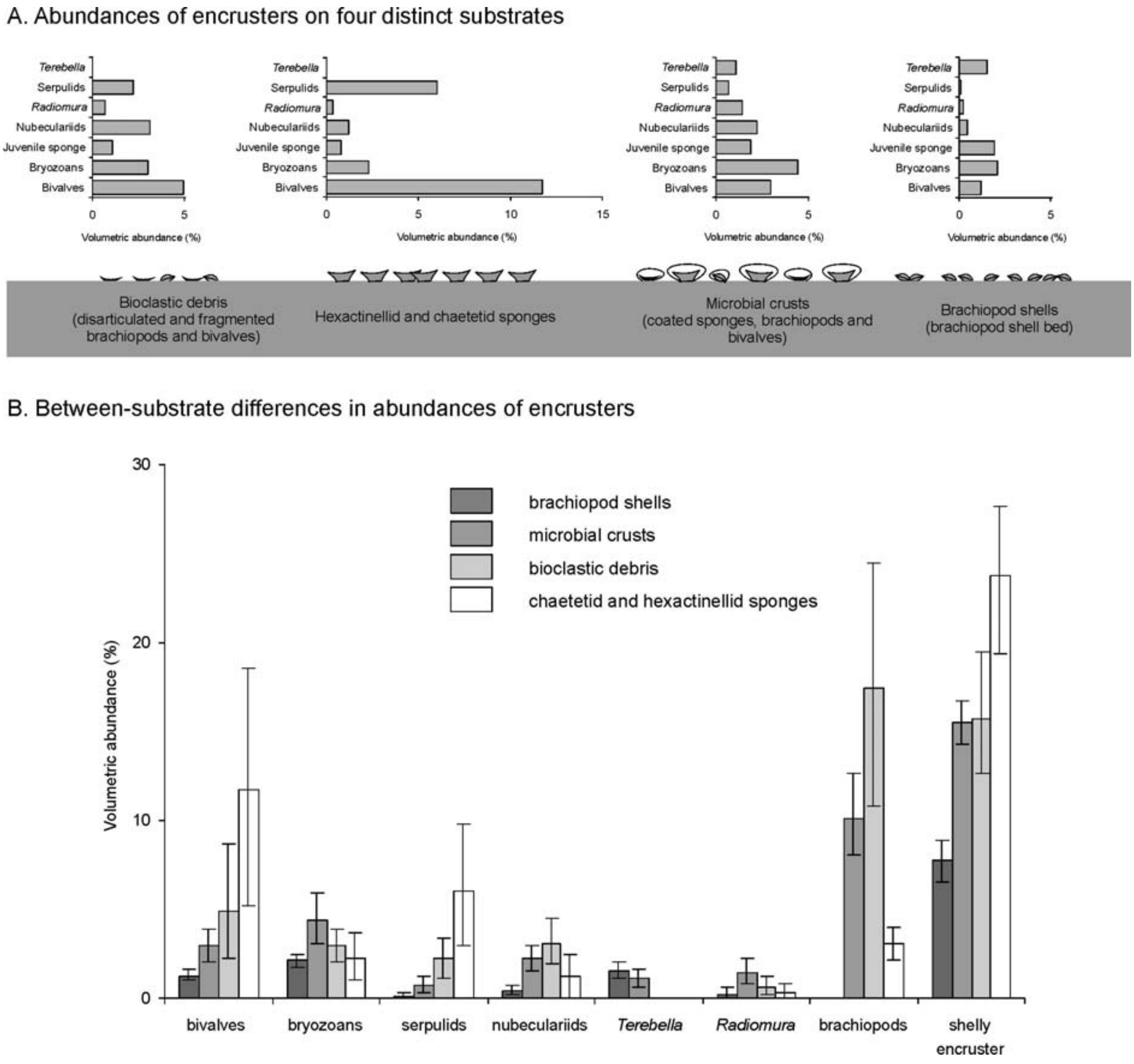


Figure 11 – A. Abundances of encrusters on four substrate types. B. Between-substrate differences in volumetric abundances of the encrusters with 95% bootstrapped confidence intervals.

Borers

Microborers are very rare or absent in the lower member of the Foum Zidet Formation. Macroborers represented by lithophagid bivalves and the haplosclerid sponge *Aka* are relatively common. Both borers are restricted to originally calcareous substrates or siliceous sponges that were rapidly replaced by calcite (Reitner and Keupp, 1991; Delecat et al., 2001). Interestingly, *Aka* and boring bivalves commonly occur together in five thin-sections and, based on presence/absence data, they both occurred in all three environments. Bivalve borings are preserved typically in massive chaetetids and large hexactinellid sponges. *Aka* bored mainly in hexactinellid sponges and microbial crusts and penetrated also brachiopod shells. Although their abundance is difficult to quantify, it seems that the frequency of *Aka* is higher in oncoidal floatstones and in the brachiopod shell bed, which originated in deeper environments. In oncoidal floatstones, borings of *Aka* are commonly infilled with an aggregation of aligned sponge spicules. In addition, aggregations of non-rigid sponges are locally preserved in shell cavities of brachiopods in oncoidal floatstones and in the brachiopod shell bed.

Separation of temporal and spatial effects on component abundance

As follows from one-way ANOSIM analyses, both temporal factors and spatial factors show some correlation with abundance patterns of the biotic groups (although differences among the environments were rather low). In order to test temporal and spatial effects separately, two-way crossed design is used here. With two-way crossed ANOSIM (Warwick et al. 1990; Warwick and Clarke 1991; Clarke 1993) the relationship between the abundance pattern and one factor (e.g., time) can be tested by removing the variation caused by another factor (e.g., environment).

The results of two-way crossed ANOSIM with respect to the within-unit differences among the environments are remarkable and contrast with the results of one-way ANOSIM. The differences among the three environments are higher and significant (R = 0.486, p = 0.0004) and the pairwise comparisons indicate that environments below MSWB significantly differ in their component abundances from environments above NSWB (R = 0.729, p = 0.001) and below NSWB (R = 0.409, p =0.014). This result is graphically shown in Figure 12, where environmental transects with component abundances are given for four depositional units (units 2-3 and units 4-5 were pooled into two units in this analysis). It means that regardless of the temporal variation in environmental factors, the components show differential abundances among the environments. Bivalves consistently occupy the shallowest portions of the environmental transect. Brachiopods may dominate in each environment but when co-occurring with hexactinellids and microbial crusts along the environmental transect, they are more common in shallow environments. Hexactinellids predominate in environments below NSWB and MSWB in sponge-dominated units 2 and 3, and microbial crusts are consistently more common in environments below MSWB.

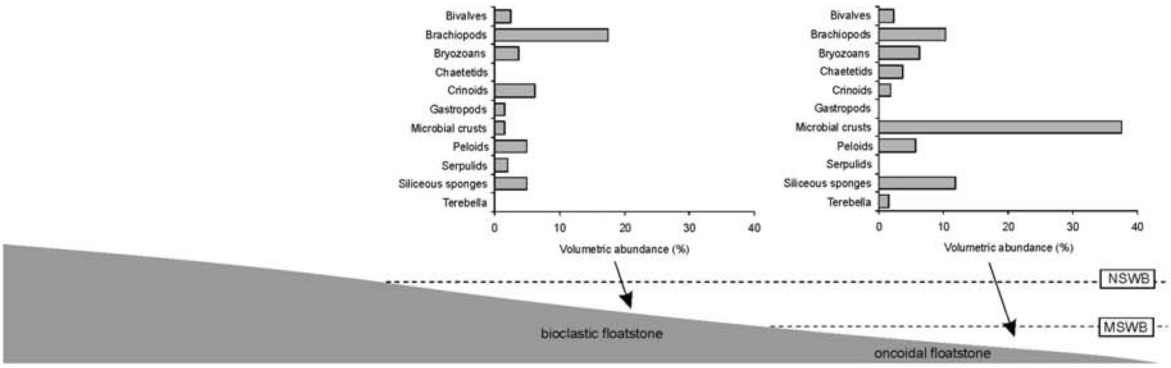
.

Two-way ANOSIM (habitat effects on components, allowing for temporal effects)	R	p-value (alpha = 0.05/3)	Number of permutations	Number of permuted R≥observed R
Global test	0.486	0.0004	10000	4
Pairwise tests:				
Below NSWB, Below MSWB	0.409	0.014	10000	137
Below NSWB, above NSWB	0.311	0.071	350	25
Below MSWB, above NSWB	0.729	0.001	840	1

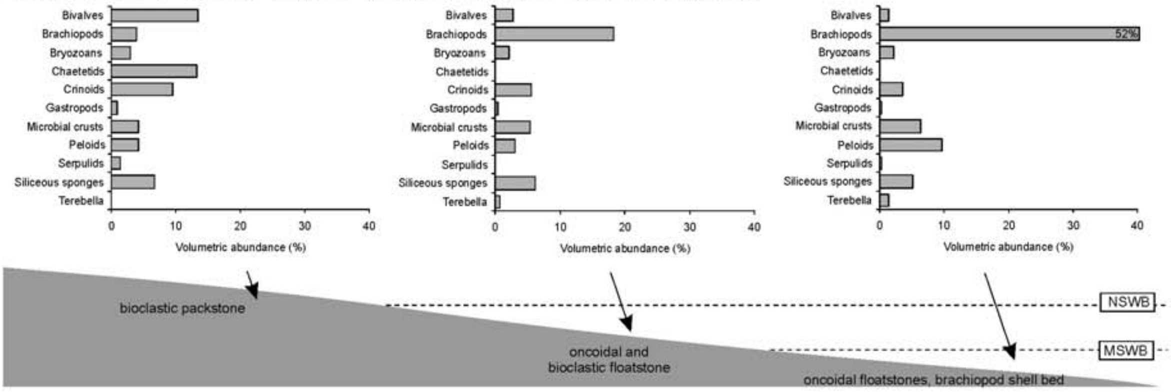
Two-way ANOSIM (temporal effects on components, allowing for habitat effects)	R	p-value (alpha = 0.05/6)	Number of permutations	Number of permuted R≥observed R
Global test	0.511	0.0002	10000	2
Pairwise tests:				
microbialite unit 1 vs. sponge units 2-3	-0.119	0.500	50	25
microbialite unit 1 vs. bioclast units 4-5	0.637	0.015	336	5
microbialite unit vs. microbialite unit 6	0.37	(0.114)	35	4
sponge units 2-3 vs. bioclast units 4-5	0.61	0.0008	10000	8
sponge units 2-3 vs. microbialite unit 6	0.49	0.017	175	3
bioclast units 4-5 vs. microbialite unit 6	0.623	0.010	840	8

Table 3 - Results of two-way crossed analyses of similarities that separate temporal and spatial (environment) effects on abundances of components.

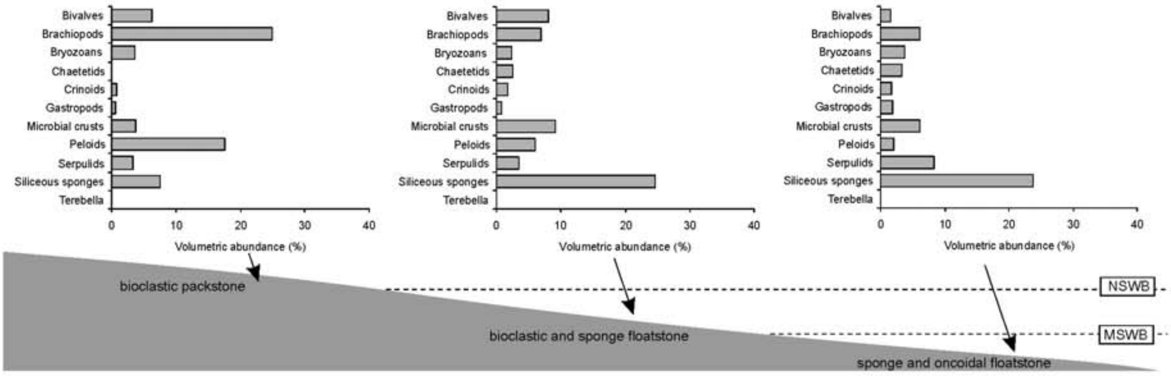
D. Microbial-dominated unit 6 (lower member of the Foum Zidet Formation)



C. Bioclast-dominated units 4 and 5 (lower member of the Foum Zidet Formation)



B. Sponge-dominated units 2 and 3 (lower member of the Foum Zidet Formation)



A. Microbialite-dominated unit 1 (lower member of the Foum Zidet Formation)

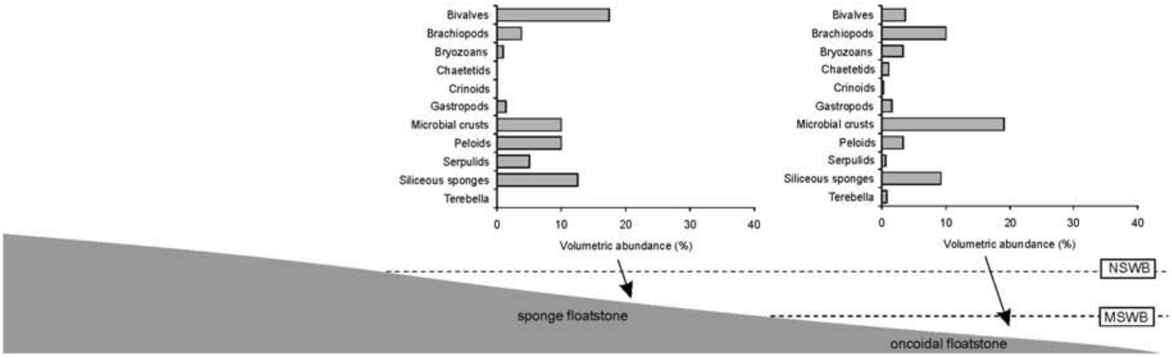


Figure 12 – Temporal variations in abundance of components along the environmental transect during four time intervals. A. Microbialite-dominated unit 1. B. Sponge-dominated units 2-3. C. Bioclast-dominated units 4-5. D. Microbialite-dominated unit 6. Note that the deepest environments below MSWB are dominated by different biotic groups at different time intervals.

Furthermore, the differences within environments among depositional units are more pronounced with two-way than with one-way analysis (Tab. 3). As is visible in Figure 12, bivalves, brachiopods, hexactinellid sponges and microbial crusts changed their environmental preference in time. In environments below MSWB, hexactinellid sponges dominated in units 2-3 and brachiopods in units 4 and 5. In other units, microbial crusts were more abundant than hexactinellid sponges and brachiopods in environments below MSWB. In environments above and below NSWB, bivalves, brachiopods and hexactinellids replace each other in dominance through time. This means that environmental preferences of the main biotic groups with respect to the level of wave base varied through time. These temporal variations in preferences result in poor performance of one-way analyses because they obscure differences among environments.

Relationship between encrusters and microbial crusts

Results. Microbial crusts are represented either by laminar, dense and peloidal crusts that form asymmetric oncoids, commonly coalescing into each other, or by structurless dense micritic coatings or infillings that are mainly present in shell cavities, shell shelters and within sponges. In terms of 95% confidence intervals, thickness of microbial crusts significantly increases towards the deeper environments below MSWB (Fig. 13). This environmental preference, together with abundant cryptic crusts and asymmetric in situ growth indicates that the growth of microbial crusts was probably light independent.

The relationship between the thickness of microbial crusts and their possible competitors is tested by comparing the mean thickness of microbial crusts with abundance of several biotic groups (Fig. 14, Tab. 4). Brachiopods, hexactinellid and chaetetid sponges, encrusting bivalves, bryozoans, and serpulids are the most probable candidates that would restrict or stop growth of microbial crusts via overgrowth or smothering. Therefore, their abundance is compared with microbial crust thickness. Although grazing gastropods belong to one of the most important groups that potentially destroy microbial crusts, their abundance pattern is not analyzed because they are very rare in the Foum Zidet Formation. The abundances of biotic groups are volumetric percentage estimations from thin-sections but they do not sum up to 100 because the samples contain abundant micrite. There is also no significant correlation between abundance of microbial crusts and micrite abundance ($r = -0.18$, $p = 0.35$) and between mean crust thickness and micrite abundance ($r = 0.03$, $p = 0.89$). Therefore, the correlations investigated below should not be spurious artifacts due to the percentage sum effect. The mean thickness of microbial crusts significantly negatively correlates with the abundance of bivalves (Spearman rank corrrelation, $r = -0.505$, $p = 0.0044$) and serpulids ($r = -0.793$, $p < 0.0001$). The negative correlation between the mean thickness of microbial crusts and chaetetids ($r = -0.39$, $p = 0.0312$) and hexactinellids ($r = -0.347$, $p = 0.06$) is lower. However, there is no correlation between the mean thickness of microbial crusts and the abundance of brachiopods ($r = 0.1$, $p = 0.57$), bryozoans ($r = 0.012$, $p = 0.95$), and *Terebella* ($r = 0.25$, $p = 0.18$).

The volumetric abundances of encrusters in thin-sections can be thought as representing a measure of frequency of substrate cover or resource limitation for sessile organisms (Woodin, 1983). This measure thus provides information about the intensity of competition for space in predominantly hard-bottom habitats. The differences in the percent cover of shelly encrusters among the substrates and among the environments are evaluated here. In order to avoid circularity in substrate comparisons, hexactinellid and chaetetid sponges are not included into the abundance of shelly encrusters (with the exception of juvenile sponges). The differences in the percent cover of shelly encrusters among four substrates are significant (Kruskal-Wallis test, H = 16.9, p = 0.00073). This result is supported also by 95% bootstrapped confidence intervals (Fig. 11B). The median abundance of shelly encrusters is lowest in substrates formed by brachiopod shells (8%). Bioclastic debris (14.5%) and microbial crusts (15.5%) are characterized by moderately high abundance of shelly encrusters. Sponges are characterized by the highest median abundance of shelly encrusters (24%). This result indicates that non-microbial deposits were characterized by a higher percent cover of shelly encrusters than microbial carbonates. In contrast to the comparison among the four distinct substrates, three distinct environments show a slight increase in the mean values towards shallower environments (Fig. 8) and 95% confidence intervals indicate that the difference in the percent cover of shelly encrusters between the environments above NSWB and below MSWB is very low and of borderline significance.

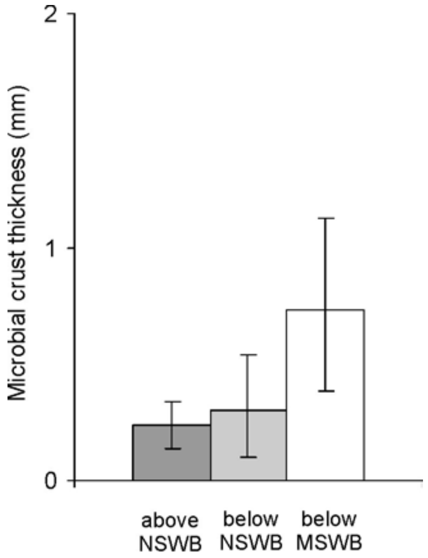


Figure 13 – Between differences among environments in mean thickness of microbial crusts with 95% bootstrapped confidence intervals show that crusts were thicker in the deeper environments.

	Spearman r	p-value
hexactinellids vs. mean crust thickness	-0.347	0.06
chaetetids vs. mean crust thickness	-0.3939	0.0312
brachiopods vs. mean crust thickness	0.107	0.57
bivalves vs. mean crust thickness	-0.505	0.0044
bryozoans vs. mean crust thickness	0.0122	0.948
serpulids vs. mean crust thickness	-0.793	<0.00001
Terebella vs. mean crust thickness	0.25	0.181

Table 4 – Summary of Spearman rank correlation coefficients for the relationship between components and mean microbial crust thickness.

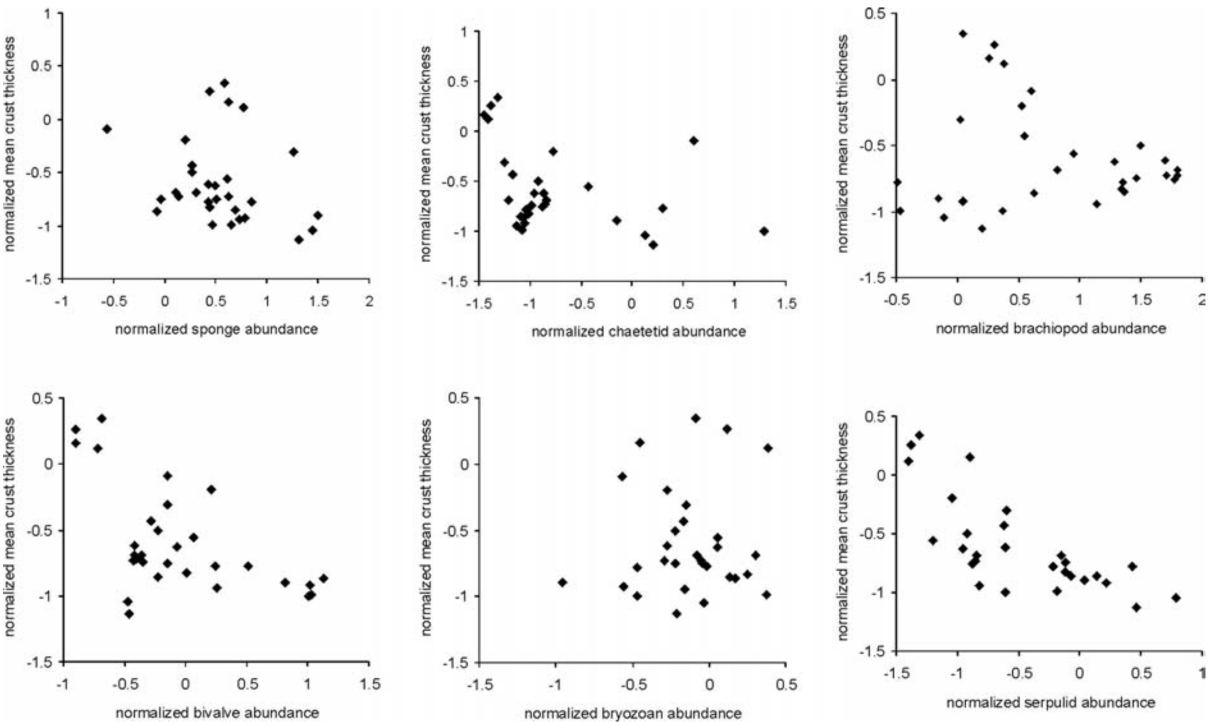


Figure 14 – Correlations between mean thickness of microbial crusts and volumetric abundance of the main biotic groups.

Discussion. The negative correlation between the abundances of shelly encrusters and microbial crust thickness and higher percentage of encruster cover in environments with less common crusts are in accord with the hypothesis that microbial crusts were excluded from the environments with intense competition for space. Although variations in abiotic factors that could change competitive abilities of encrusters and microbialites might play some role in the dominance of microbial crusts, the differences among environments in abundance of microbial crusts are thus more likely explained by variation in competition intensity rather than by between-habitat variations in microbial growth and calcification rates alone.

The negative relationship between shelly encrusters and microbial crusts could be caused by a mutually negative interaction (i.e., competition) or one-sided competitive interaction (i.e., amensalism). If competition between microbialites and shelly encrusters would be responsible for the negative correlation, the decrease in abundance of shelly encrusters in microbialite-dominated environments can be explained by the scenario of microbial fouling and overgrowth of shelly encrusters. It is implicitly assumed that the potential interaction between metazoans and microbial crusts is asymmetrical because present-day microbial crusts in cryptic marine habitats grow very slowly, approximately 0.001 - 0.0015 mm/year (Reitner, 1993). Schmid et al. (2001) estimated that the Upper Jurassic microbial mounds of the Swabian Alb could grew more rapidly, about 0.3 mm/year during their maximum development. Although growth rates of sponges, brachiopods, and bivalves are variable, they are usually higher than the estimated growth rates of microbial crusts (Thayer, 1977; Curry, 1982; Krautter et al., 2001; Whitney et al., 2005). However, small-sized clonal forms as bryozoans or solitary forms as serpulids can enter intense competition for space with microbial communities (Scholz and Hillmer, 1995; Gerdes et al., 2005).

In general, sponges and bivalves dominate in competitive hierarchy over polychaetes and bryozoans in present-day shallow marine habitats (Jackson, 1983; Dürr and Wahl, 2004; Fagerstrom et al., 2000). Small-scale stromatolite-like alternations of bryozoans with microbial crusts (i.e., bryostromatolites) are typical of environmentally-restricted habitats (Bijma and Boekschoten, 1995; Palinska et al., 1999). Bryozoans prevail during normal marine conditions and microbial crusts develop during stressful conditions. Serpulids commonly formed buildups with microbial crusts in low-energy environments below storm wave base during the Late Triassic (Berra and Jadoul, 1996; Iannace and Zamparelli, 1996; Climaco et al., 1997). Such serpulid-microbial communities are also interpreted as the evidence of high-stress environmental conditions with fluctuating salinity and oxygen concentrations that are not tolerated by less eurytopic taxa (Cirilli et al., 1999). However, serpulids of the Foum Zidet Formation did contribute to microbial buildups much less than bryozoans. Nevertheless, the association of bryozoans with microbial crusts and the lower abundance of bryozoans on substrates with higher percent cover of shelly encrusters imply that sponges and bivalves were competitively inferior and the potential competitive interaction was strongly asymmetrical.

The amensalism scenario between microbialites and shelly encrusters indicates that some environmental conditions inhibited the settlement and recruitment of shelly encrusters in the environments dominated by microbial communities. The absence shelly encrusters in microbialite-dominated environments might be linked to limited light intensity, oxygen-deficient conditions or a restricted flow regime (Leinfelder et al., 1993; Dupraz and Strasser, 2002). A generalized environmental transect of the Rich fault-block that corresponds to this scenario is shown in Figure 15. A limit in light intensity inhibiting phototrophic organisms is improbable as a potential factor enhancing the formation of microbial crusts because even the shallower environments with a lower abundance of microbial crusts and a higher abundance of heterotrophic fauna were affected by low light intensity. In deeper environments of the Central High Atlas Basin, oxygen-deficient conditions can be postulated during time intervals with restricted water mixing and/or high nutrient input, as opposed to shallower environments with higher abundances of encrusters. Although high nutrient supply alone cannot account for the exclusion of heterotrophic metazoans, it is typically associated with high particle concentrations, decreased oxygen concentrations or toxic conditions that can restrict the abundance of heterotrophs (Hallock and Schlager, 1986; Mutti and Hallock, 2003; Levin, 2003). Hypoxia connected with oxygen-minimum zone edge effects was specifically suggested by Neuweiler et al. (2001) for the massive development of sponge-microbial mounds in the upper part of the Foum Zidet Formation. Although the abundance of brachiopods, epibyssate bivalves and bryozoans in the microbial carbonates implies that the oxygen concentrations were not completely exhausted, oxygen-deficiency and a restricted flow regime might have decreased the fitness of the most common encrusters with high metabolic rates (e.g., bivalves).

Variations in sedimentation rate represent one of the most important factors determining the distribution of microbial carbonates (Leinfelder et al., 1993; Olivier et al., 2004b). However, it is probable that the environments of the Rich fault-block were not affected by variations in siliciclastic input due to their constant amount in the whole succession. Along transect, environments might have been affected by variations in the sedimentation rate of carbonate mud that could be related either to its in situ production by benthic organisms or to its input from shallow carbonate settings. Within the transect of the Rich fault-block, one of the main sources for the variation in sedimentation rates possibly was sediment winnowing and bypassing in shallower environments, which were affected by higher storm-reworking, resulting in trapping of more sediment in deeper parts of the fault-block halfgraben. The possibility that microbial crusts were inhibited by too high sedimentation rates would then be improbable because microbial crusts were more abundant and thicker in the deeper environments.

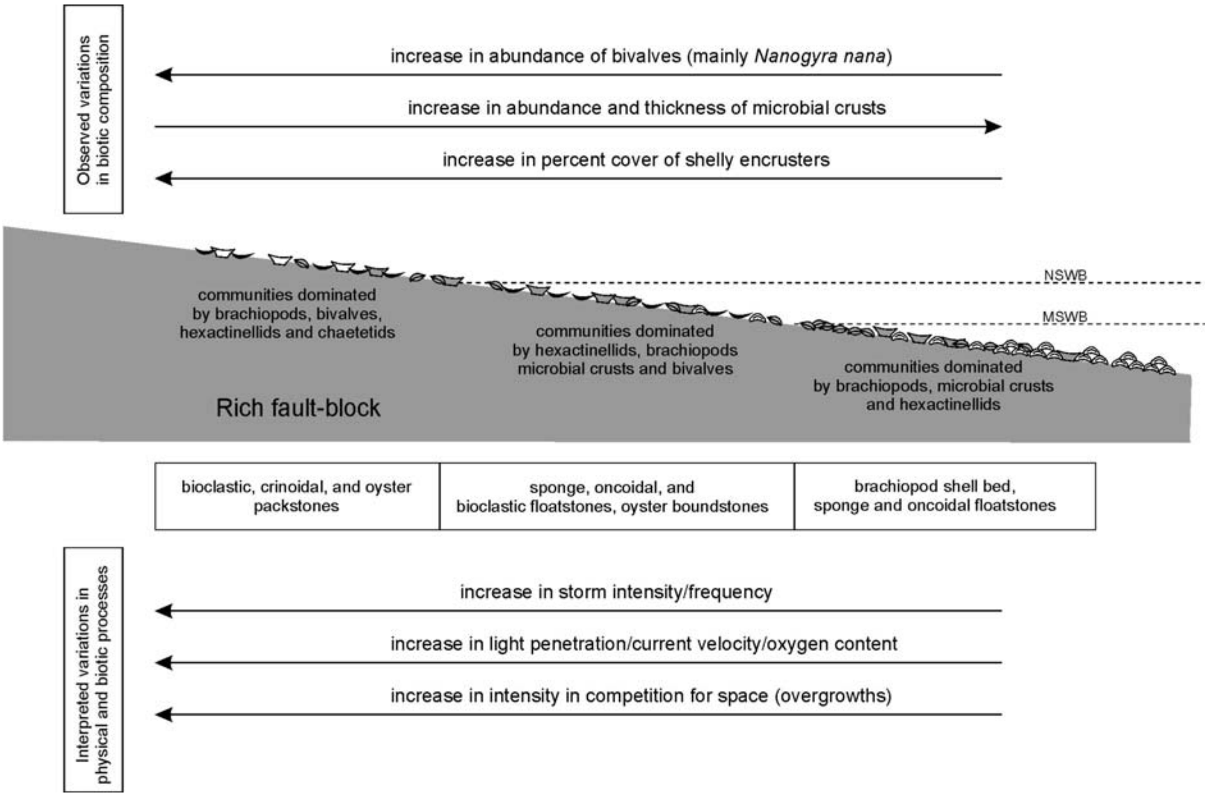


Figure 15 – Environmental transect across the Rich fault-block represented by the deposits of the lower member of the Foum Zidet Formation with simplified spatial variations in intensity of interference competition and in abiotic factors.

Brachiopod preference to microbial crusts – indicator of low interference competitive ability?

The hypothesis stating microbial benthic communities proliferated in environments with reduced intensity of competition for space is supported because thickness of microbial crusts correlates negatively with increasing percent cover of shelly encrusters. Therefore, differential abundance of benthic metazoans between environments with and without microbial crusts can be used as an indicator of their ability to compete for space or resist disturbance due to grazing. As follows from between-substrate differences in abundance of benthic metazoans, brachiopods and bryozoans preferred environments with microbial crusts, and bivalves and serpulids were more common on substrates formed by sponges and bioclastic debris. This implies that brachiopods and bryozoans had lower interference competitive abilities when compared to bivalves and serpulids. Although this implication is in accord with present-day ecology of slow-growing and poorly mobile brachiopods with low metabolic rates when compared to bivalves, independent evidence from substrate preferences substantially strengthens the argument about reduced abilities of fossil brachiopods to compete for space. Although bryozoans are supposed to be competitively inferior in comparison to polychaetes (Russ, 1982; Lopez Gappa, 1989; Barnes and Dick, 2000), serpulids can be successful competitors in encounters with bryozoans in some cases (Maughan and Barnes, 2000). This seems to be the case in the Foum Zidet Formation because serpulids were more common in environments with higher percent cover of shelly encrusters. A higher abundance of brachiopods on microbial crusts than on sponges demonstrates that brachiopods were possibly inferior interference competitors when compared to bivalves because they were more abundant in environments with lower intensity of competition for space.

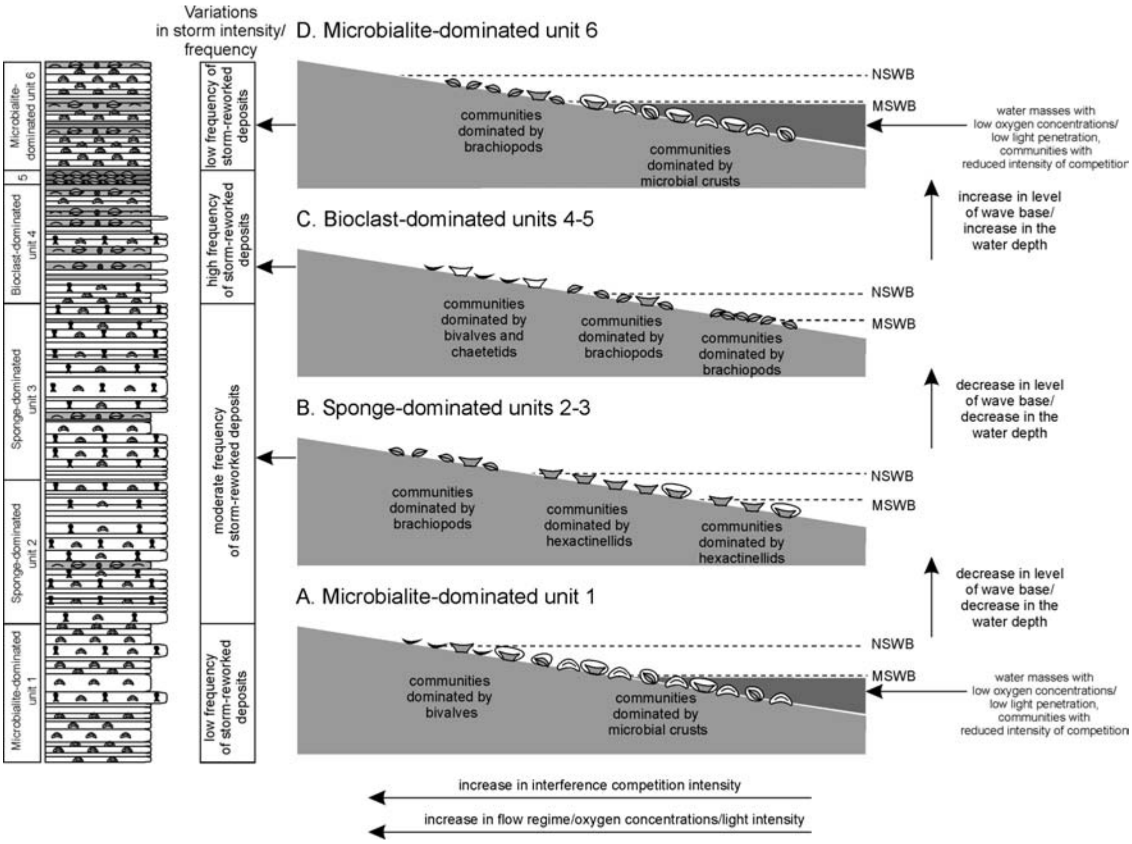


Figure 16 – Interplay of biotic and abiotic factors determining composition of microbial-sponge communities during deposition of the lower member of the Foum Zidet Formation.

Interplay between biotic and abiotic factors

Spatial differences in the abundances of microbial crusts and shelly encrusters indicate the prominent role of reduced intensity of competition in habitats with microbial communities, although the relationship between crusts and encrusters was probably one-sided or asymmetric. Microbial crusts were outcompeted in open marine habitats by metazoan shelly encrusters but the encrusters were more probably inhibited by abiotic factors in the habitats dominated by crusts. Temporal differences in the abundances of microbial crusts and shelly encrusters correlating with a long-term trend in the wave base level hint at possible abiotic factors accounting for rare shelly encrusters in habitats dominated by microbial crusts (Fig. 16). Variations in the level of wave base probably affected the overall hydrodynamic conditions and water mixing patterns on the Rich fault-block. During time intervals with a high level of wave base, restricted water circulation may have led to a decrease in oxygen concentration in the deepest environments that limited shelly encrusters. In accord with this, microbial crusts are typical of the units with low frequency of storm-reworked deposits and dominate in deep environments characterized by low-energy hydrodynamic conditions. During time intervals with a falling level of wave base, water mixing and oxygen concentrations increased and intensity of competition was probably high also in the deepest environments. During such conditions, which are represented by sponge-dominated units 2-3 and bioclast-dominated units 4-5, microbial crusts were rare even in the deepest environments. The increase in the abundances of metazoans and the decrease in abundance of microbial crusts thus probably reflect changes in abiotic factors that correlated with increasing within-basin water mixing and increasing oxygen concentrations.

Conclusions

(1) The benthic fauna of the lower member of the Foum Zidet Formation shows distinct spatial distribution patterns with respect to inferred storm wave base, although environmental preferences of the main biotic groups change through time. Bivalves consistently increase in abundance and microbial crusts decrease in abundance towards shallow environments. Shelly encrusters are characterized by distinct substrate preferences, with bivalves and serpulids dominating on sponge substrates and bryozoans dominating on microbial crusts. Abundance of shelly encrusters and their percent cover negatively correlate with the mean thickness of microbial crusts, indicating that microbial communities dominated in environment with lower competition intensity. The competitive hierarchy can be characterized as sponges and bivalves > serpulids > bryozoans and microbial crusts. Higher abundance of brachiopods on substrates formed by microbial crusts than on sponges indicates that brachiopods preferred substrates with reduced intensity of competition for space.

(2) Temporal variations in environmental preferences of the main biotic groups correlate with temporal trends in average level of wave base, possibly related to variations in water mixing and circulation patterns. At times of falling wave-base level, deep environments were dominated either by hexactinellids or brachiopods, and microbial crusts were rare. At times of rising wave-base level, deep environments were dominated by microbial crusts, and hexactinellids and brachiopods decreased in abundance. This temporal pattern indicates lower competition intensity and unfavorable conditions for shelly encrusters in the deeper environments under conditions of restricted water mixing, leading to extensive growth of microbial crusts. Under such conditions, shelly encrusters were excluded by restricted flow regime and decreased oxygen concentrations. This scenario suggests combined effects of biotic interactions and abiotic factors on formation of sponge-microbial deposits during the Early Jurassic.

8. Life history strategies of Early Jurassic brachiopods and bivalves: differential response to flow speeds and resource limitation

(with Franz T. Fürsich and M. Wilmsen)

Abstract. Linking abundance with survivorship in this study enables to evaluate whether distribution patterns of brachiopods and bivalves inhabiting sponge-microbial biostromes of the Foum Zidet Formation (Sinemurian) are in accord with the hypothesis of adaptively anachronistic brachiopods being displaced into competition-free habitats. Cementing bivalves increased and brachiopods decreased in abundance towards shallow habitats above storm wave base. The cementing oyster *Nanogyra* reached high community-level abundance, low juvenile mortality and high adult median size on sponge substrates. In contrast, brachiopods attained low community-level abundance, high juvenile mortality and low adult median size on sponge substrates. Juvenile mortality rates of *Nanogyra* correlate negatively with abundances of adult pedunculate brachiopods, and juvenile mortality rates of the brachiopod *Zeilleria* correlate negatively with abundances of adult *Nanogyra*. Brachiopods formed shell beds owing to substantially reduced mortality rates because their density positively correlated with high juvenile survivorship and high median adult size. In contrast, thin concentrations of *Nanogyra* probably reflect short-lived patches on substrates resulting from massive recruitment because its shell density did not show any relationship to mortality and size patterns. Between-habitat differences in abundance and mortality patterns between brachiopods and bivalves are explained as differential response to variations in flow speed owing to their different pumping and clearance rates. Between-substrate differences can be explained as competitive, juvenile-adult interactions for depleted space under moderate flow speeds, and possibly for depleted food under reduced flow speeds. Shallow habitats characterized by higher flow speeds and higher percent cover of encrusters on sponge substrates were probably characterized by high intensity of competition for space. Brachiopod juveniles might be overgrown in such habitats by fast-growing faunal elements, and *Nanogyra* was able to rapidly exploit space owing to its opportunistic population dynamics. This is in accord with a competitive superiority of bivalves. However, brachiopods were more efficient than *Nanogyra* in feeding under reduced boundary-layer flow in deep habitats. Dense brachiopod populations indicate that brachiopods either depleted food resources under reduced flow speeds, being competitively superior to cementing bivalves, and/or possessed specific feeding and physiologic adaptations for living in flow- and food-limited conditions. Both options are inconsistent with the hypothesis that adaptively anachronistic brachiopods are restricted to competition-free habitats.

Introduction

Sponge-microbial communities were widespread on carbonate ramps during the Triassic and Jurassic (Flügel, 2002; Leinfelder et al., 2002). These communities were inhabited by diverse brachiopods that locally formed a dominant component among non-clonal (unitary) benthic invertebrates in terms of their community-level abundance. For example, brachiopods are almost invariably present in sponge-microbial reefs that were extensively developed on the northern margin of the Tethys during the Late Jurassic (Leinfelder et al., 1994; Werner et al., 1994; Brugger, 1999; Reolid, 2005). Although sponge-microbial reefs were less widely distributed during the Early Jurassic, brachiopods were numerically common in such habitats and locally formed autochthonous shell beds on the SW margin of the Tethys ocean (Hauptmann, 1990; Milhi, 1992; Mehdi et al., 2003; Tomašových et al., 2006). This proliferation of brachiopods in sponge-microbial reefs might be related to some unique combination of abiotic or biotic factors that were associated with, or produced by, sponge-microbial reefs. Given the abundance of hard substrates, the relatively low abundance of epifaunal bivalves in such habitats is surprising. Sponge-microbial carbonate ecosystems do not have comparable counterparts in the present-day seas and the ecology of their non-clonal benthic inhabitants is poorly constrained. Present-day reefs formed by siliceous sponges on the Western Canadian continental shelf differ from fossil sponge-microbial communities because they trap and baffle siliciclastic sediment and do not form in a carbonate regime (Krautter et al., 2001; Whitney et al., 2005).

Brachiopods and epifaunal bivalves are preserved in a relatively uniform sequence of micrite-rich sponge-microbial carbonates in the lower member of the Foum Zidet Formation (*Asteroceras obtusum* Zone, Sinemurian; Wilmsen et al., 2002) in the Central High Atlas. These deposits were deposited above and below maximum storm wave base. They were not affected by any substantial variations in rate of siliciclastic supply, land-derived nutrient supply or substrate stability, which usually play an important role in controlling the distribution of suspension-feeders. Constraining their effects, this uniformity thus enables to analyse effects of other abiotic or biotic factors on distribution patterns of brachiopods and bivalves. Infaunal bivalves do not occur in the Foum Zidet Formation. Available taphonomic and ecologic data are inconclusive whether their absence represents a primary ecologic signal (e.g., due to abundance of hard substrates) or taphonomic bias (i.e., preferential destruction of aragonitic shells). A general goal of this chapter is to assess the distribution, abundance and survivorship patterns and survivorship of brachiopods and *epifaunal* bivalves that occupied sponge-microbial ecosystems during the Early Jurassic, and to develop a predictive scenario that explains abundance and distribution of brachiopods in such environments. A simplified hypothesis on the distribution of brachiopods and bivalves states that energy-minimalistic brachiopods were out-competed by bivalves with higher metabolic rates and with superior interference and exploitation competitive abilities on hard substrates during the Mesozoic (Thayer, 1985), and that adaptively anachronistic brachiopods were displaced into "safe" enemy-free habitats (Vermeij, 1987). Increased predation intensity during the Mesozoic probably does not account for the decreasing abundance of brachiopods, because of the low nutritional value and unpalatability of brachiopods (Thayer, 1985; Thayer and Allmon, 1990; Mahon et al., 2003), low frequency of sublethal shell breakage (Alexander, 1986), and low drilling frequency on shells of post-Paleozoic brachiopods (Kowalewski et al., 2005).

In this chapter, it is evaluated whether habitats with abundant brachiopods represent habitats with reduced competition intensity as compared with habitats dominated by epifaunal bivalves. Two combined approaches are performed to address the ecology of brachiopods and epifaunal bivalves. The first one focusses on the community ecology of brachiopods and bivalves. Their abundance patterns are analysed with respect to time and with respect to varying wave-base level and substrate composition. The second approach is devoted to population ecology and is based on size-frequency distributions of brachiopods and bivalves. Survivorship curves are analysed to evaluate differences in life history strategies of brachiopods and bivalves between habitats, between substrates and between assemblages with low and high shell density. Although variation in recruitment and growth rates are not constrained, joint use of community-level and population-level data enables to (1) estimate the relationship between mortality and abundance in brachiopods and bivalves, and (2) to evaluate whether high shell density in brachiopods and bivalves is related either to high rate of increase in population size (i.e., opportunistic “boom-and-bust” dynamics) or to populations with low mortality living near their carrying capacity.

Methods

Untransformed relative abundances of brachiopod and bivalves from 39 samples were used in exploratory and confirmatory multivariate analyses with a minimum sample-level number of 36 specimens. Brachiopods and bivalves are silicified and individual samples of compact limestones about 250 g in weight were dissolved with diluted hydrochloric acid and sieved through a 0.1-mm mesh sieve. All determinable bivalve and brachiopod specimens up to 0.5 mm in size were collected under a binocular microscope using 25x magnification. The abundances were converted into number of individuals as the sum of articulated specimens plus the dominating number of either brachial or pedicle valves. Discrimination of groups of samples with similar taxonomic abundances was performed on species level. Non-metric multidimensional scaling (NMDS) analyses were based on species, genus and guild abundances. Due to a stratigraphic species replacement of *Zeilleria*, one of the most abundant brachiopod genera, generic abundances were used for testing differences in community composition among habitats and among time intervals. The analyses were performed with (1) the complete dataset, and with (2) six restricted mesh sizes, excluding the smallest specimens and juveniles smaller than 1, 2, 3, 4, 5 and 6 mm. In this chapter, most of the analyses were performed either with the complete dataset, or with the restrictive dataset excluding specimens smaller than 5 mm (i.e., mesh size > 5 mm). The differences in community composition were tested with respect to temporal and environmental subdivision of samples. The temporal subdivision includes five time segments (i.e., microbial-dominated unit 1, sponge-dominated units 2 and 3, bioclast-dominated units 4 and 5 and microbial-dominated unit 6). Deposits with fossil assemblages were assigned to three habitats: (1) Amalgamated packstones and rudstones were assigned to habitats above normal storm wave base (NSWB), (2) bioturbated, micrite-rich beds alternating with thin packstone layers to moderate-energy habitats between NSWB and maximum storm wave base (MSWB), and (3) micrite-rich floatstones to low-energy habitats below MSWB. In addition, the deposits were subdivided according to dominant components into three substrates: (1) sponge substrate, (2) microbial crust substrate, and (3) substrate formed by brachiopod-bivalve debris and shells. To avoid circular reasoning, brachiopod shell beds were assigned to the third substrate type.

Size-frequency distributions (SFD) were analysed in terms of their median size, skewness and kurtosis. Multivariate ordination is used for analysing the differences between SFDs (Kowalewski and Demko, 1997). NMDS is evaluated here for this purpose. The between-habitat and between-substrate differences are tested with analysis of similarities (ANOSIM), which is based on the Manhattan distance matrix. The Manhattan distances are based on the percentage abundances of 1 mm size classes. Using Euclidean distances or Bray-Curtis dissimilarities as a measure for the resemblance matrix for NMDS and ANOSIM, the results were highly equivalent to those based on Manhattan distances. Although the observed mortality rates of juveniles do not represent the real mortality rates due to size-specific taphonomic processes and time-averaging, it is assumed that the size-selective taphonomic processes affected brachiopod and bivalve size-frequency distribution similarly across all samples. This assumption is backed up by abundant thin-shelled, small-sized adults or juveniles 1-2 mm in size in all analysed samples. Therefore, the differences in observed mortality rates between habitats and between substrates are interpreted in comparative terms.

Although the death assemblages are time-averaged to some degree and thus represent several cohorts from different time intervals, estimation of size-specific mortality rates (q_x) based on size-frequency distribution of death assemblages are computed from life tables as if the individuals were members of one cohort (Krebs, 1999). The input data are represented by number of individuals that died within mm-size interval x to x + 1 (d_x). Number of individuals of a cohort alive at the start of size interval x is

$$n_{x+1} = n_x - d_x$$

Proportion of individuals surviving at the start of size interval x (l_x) is computed as

$$l_x = n_x/n_0$$

Logarithm of l_x is used for construction of survivorship curves. Finite rate of mortality (q_x) during the size interval x to x + 1 is

$$q_x = d_x/n_x$$

Although maximum shell size differs among the most abundant brachiopods and bivalves, juvenile mortality rates and juvenile survivorship are calculated for specimens smaller than 5 mm. Similarly, median adult size is calculated for specimens larger than 5 mm.

The relationship between shell density and population dynamics was evaluated in terms of juvenile mortality and adult median size. Shell density of life assemblages is a function of population dynamics that consist of two components, including variations in recruitment and mortality. Shell density of death assemblages is also affected by varying shell-destruction rates and sedimentation rates. Deposits of the Foum Zidet Formation were probably affected by minimum variations in sedimentation rates and the observed shell density is strongly related to the hardpart-input rate (Tomašových et al., 2006). The shell destruction rate probably positively co-varied with the dead-shell production rate and the observed differences in shell density are assumed to reflect primary variations in population dynamics. Juvenile mortality rate was measured as survivorship of individuals larger than 5 mm. It corresponds to a proportion of individuals (l_x) surviving at the start of size interval 5 mm. Adult median size was computed for individuals larger than 5 mm. Samples were assigned to two categories based on a qualitative field-based scoring of shell packing density (shelliness): (1) samples with dispersed and loose packing (i.e., shell-poor samples), and (2) samples with loose to dense and dense packing (i.e., shell-rich samples). Shell density was separately assigned to terebratulids (*Zeilleria*), spiriferinids (*Liospiriferina*) and oysters (*Nanogyra*). With an exception of small-scale clumps, the rhynchonellid *Squamirhynchia* does not form loosely or densely packed shell concentrations.

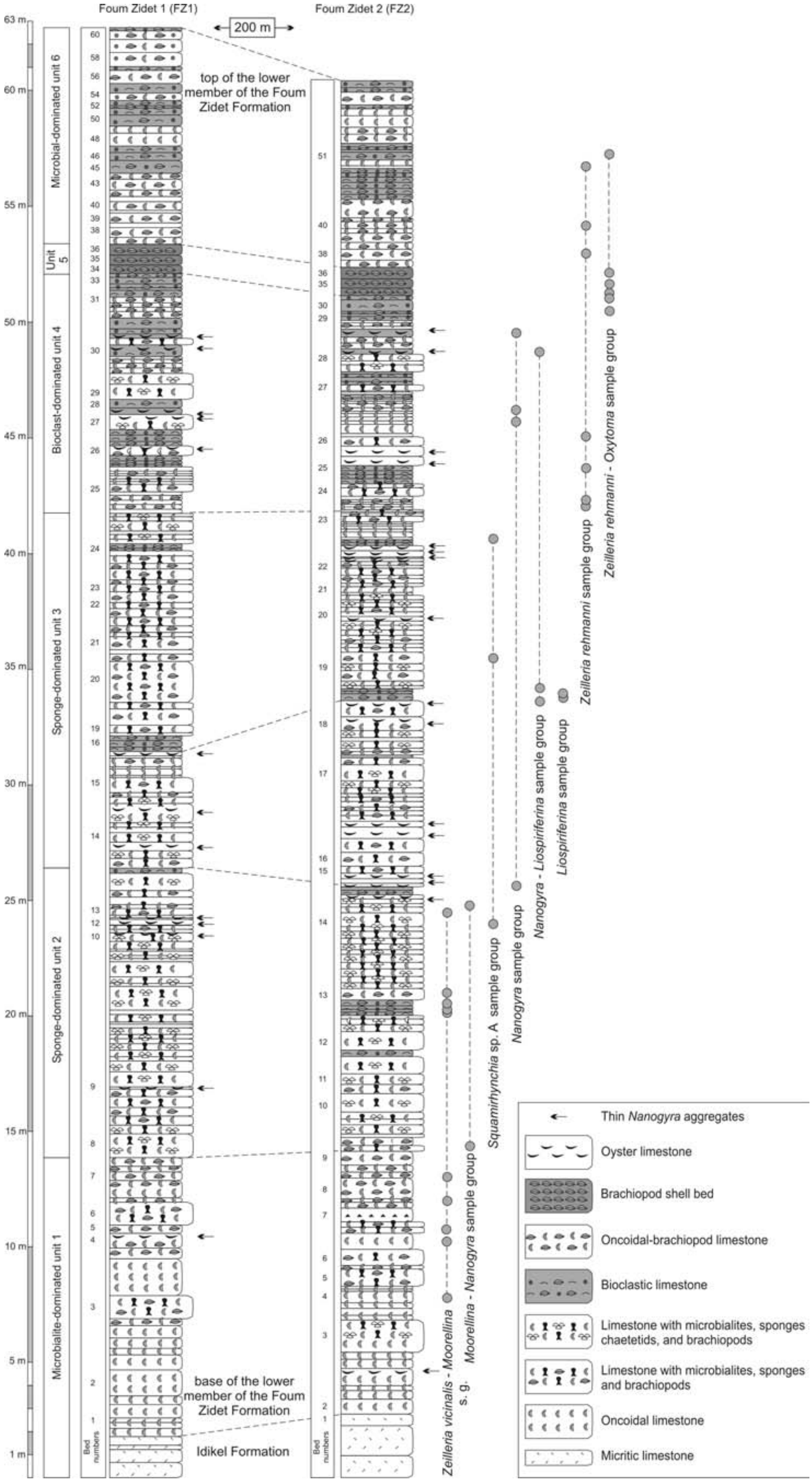


Figure 1– Foum Zidet sections showing the subdivision of the lower member of the Foum Zidet Formation into six depositional units and the temporal distribution of eight sample groups dominated by brachiopods and bivalves.

Sections

An about 60 m-thick lower member of the Foum Zidet Formation (Mehdi et al., 2003) was sampled in two sections at Foum Zidet (Fig. 1), with a distance between section of about 200 m. The member consists of well-bedded, biomicritic packstones, floatstones, and boundstones with varying amounts of hexactinellid and chaetetid sponges, microbial crusts, brachiopods, bivalves and crinoids. It was subdivided into six depositional units, including microbial-dominated unit 1, sponge-dominated units 2 and 3, bioclast-dominated units 4 and 5, and microbial-dominated unit 6. Bioclast-dominated unit 5 corresponds to a unique, 150 cm-thick shell bed with in situ brachiopods (Mehdi et al., 2003; Tomašových et al., 2006). The member is underlain by laminated and fenestrae-bearing mudstones and wackestones of the Idikel Formation, and overlain by argillaceous mudstones and marly limestones of the middle member of the Foum Zidet Formation (Mehdi et al., 2003).

Discrimination of sample groups

Eight sample groups were discriminated with a Q-mode cluster analysis of 39 samples with 8536 individuals using the group-average linking method and Bray-Curtis similarity (Fig. 2). Four sample groups are dominated by brachiopods, one sample group is dominated by the oyster *Nanogyra nana* and three sample groups are dominated by brachiopods and bivalves (Figs. 3-4). These sample groups are equivalent to the associations of Fürsich (1977) and community types of Bambach and Bennington (1996).

(1) The *Zeilleria vicinalis – Moorellina* sample group is represented by ten samples with 2921 individuals. The sample-level richness (S) varies between 5 and 11 species, the evenness (PIE) is moderately high (0.65-0.82). It is dominated by the terebratulid *Zeilleria vicinalis* (27.7%) and the thecideid *Moorellina* sp. (24.7%). The spiriferinid *Liospiriferina rostrata* (17.2%), rhynchonellids *Gibbirhynchia moghrabiensis* (9.5%) and *Squamirhynchia* sp. A (8.1%), and the cementing pseudolamellibranch *Nanogyra nana* (6.3%) are less common. Cementing filibranchs (1.1%), epibyssate (0.5%), free-lying (0.3%), and endobyssate filibranchs (0.2%) are rare. The sample group occurs in bioclastic and oncoidal floatstones, locally with dispersed sponges, in units 1-2 (Fig. 5A). These deposits correspond to habitats below NSWB and MSWB.

(2) The *Moorellina – Nanogyra* sample group is represented by two samples with 499 individuals. Its sample-level richness (S) ranges between 8 and 15 species, the evenness (PIE) is moderately high (0.59-0.68). It is dominated by the cementing brachiopod *Moorellina* sp. (51.1%), followed by the cementing pseudolamellibranch *Nanogyra nana* (28.6%). Pedunculate brachiopods are less common (12.9%), represented by *Dispiriferina* sp. (3.5%), *Zeilleria* sp. A (2.7%), *Squamirhynchia* sp. A (2.2%), *Liospiriferina* sp (1.9), and *Zeilleria vicinalis* (1.7%). Cementing (4%) and epibyssate filibranchs (2.1%) are rare. This group occurs in sponge floatstones with chaetetids, locally with thin microbial coatings, in unit 2. They correspond to habitats below NSWB.

(3) The *Squamirhynchia* sp. A sample group is defined on the basis of three samples with 870 individuals. The sample-level richness (S) varies between 6 and 11 species, the evenness (PIE) is low to moderate (0.32-0.62). *Squamirhynchia* sp. A dominates in this sample group (68.3%), followed by the far less common cementing filibranchs *Plicatula* sp. (6.9%) and *Atreta* sp. (5.4%), the pedunculate brachiopods *Liospiriferina rostrata* (6%) and *Zeilleria vicinalis* (5.1%), and the cementing

pseudolamellibranch *Nanogyra nana* (4.1%). Cementing brachiopods (0.6%), and epibyssate (0.5%) and endobyssate filibranchs (0.2%) are rare. This sample group occurs in floatstones with dispersed to loosely-packed sponges and rare microbial crusts (Fig. 5D) in units 2 and 4. They correspond to habitats below MSWB. *Squamirhynchia* occurs in clumps formed by 5-10 shells that are spatially limited to chaetetid and hexactinellid sponges (Fig. 6C-F).

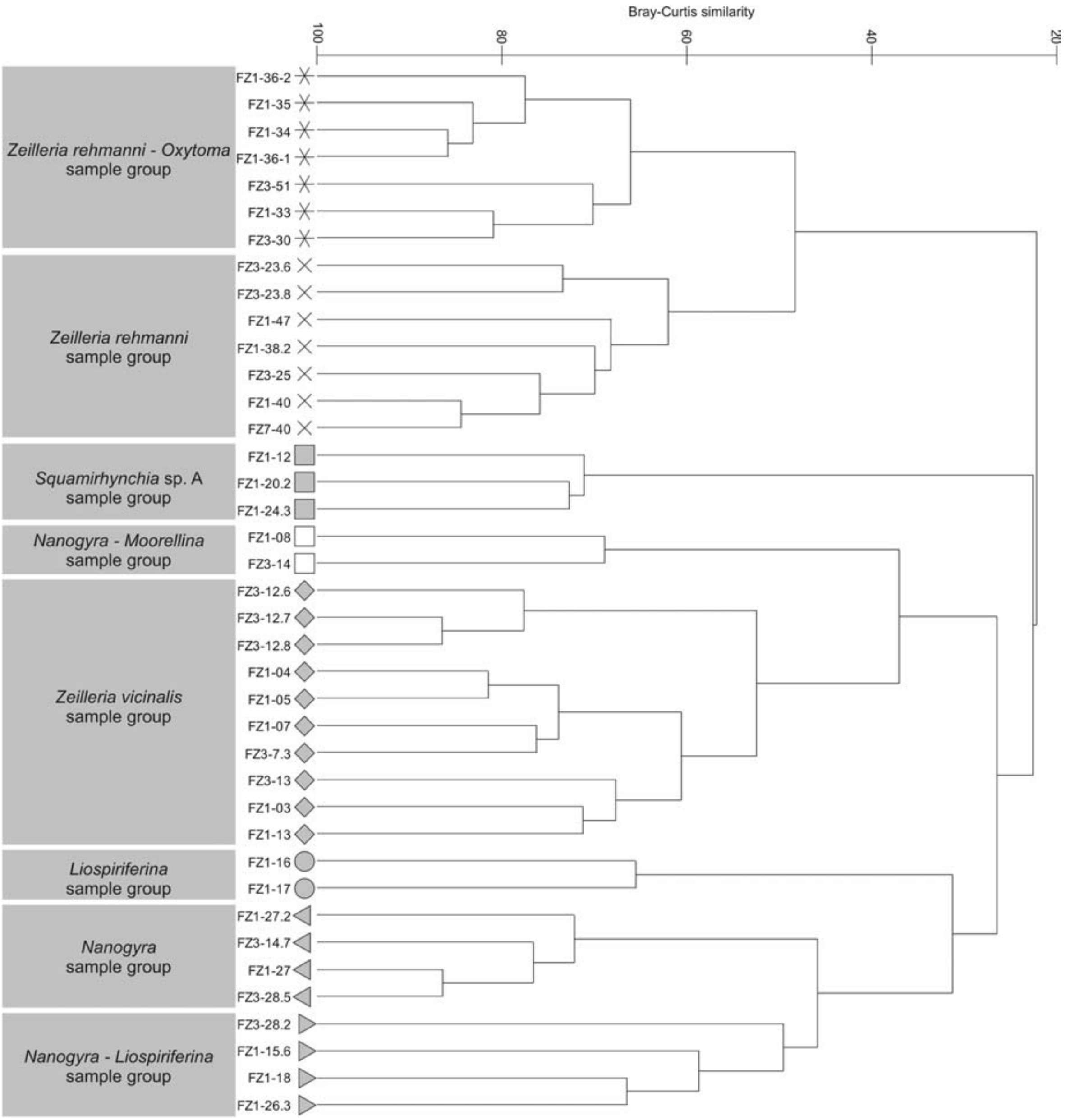


Figure 2 – Eight sample groups discriminated by Q-mode cluster analysis performed with the group-average linking method and Bray-Curtis similarity. The analysis was based on relative abundances of brachiopod and bivalve species in the complete dataset (all sieves).

(4) The *Nanogyra* sample group is represented by four samples and 796 individuals. Its sample-level richness (S) is between 8 and 10 species, the evenness (PIE) is low to moderate (0.36-0.61). *Nanogyra nana* dominates (71.8%). The rhynchonellid *Squamirhynchia* sp. A (9.4%), the inarticulate brachiopod *Discinisca* sp. (5.4%), and the spiriferinid *Liospiriferina rostrata* (4.7%) are common. Free-lying filibranchs (1.7%), cementing brachiopods (1.1%), cementing filibranchs (0.5%)

and endobyssate (0.2%), and epibyssate filibranchs (0.1%) are rare. This group occurs in bioclastic floatstones, bioclastic packstones, and floatstones with siliceous and chaetetid sponges. In the latter facies, *Nanogyra* forms thin, one or two-valve thick aggregates attached to sponges (Fig. 6A-B). The deposits represent habitats above and below NSWB. This group occurs in units 3 and 5.

(5) The *Nanogyra – Liospiriferina* sample group is defined on the basis of four samples with 1203 individuals. The sample-level richness (S) varies between 6 and 17 species, the evenness (PIE) is relatively high (0.73-0.81). *Nanogyra nana* (33.1%), *Liospiriferina rostrata* (16.6%) and *Squamirhynchia* sp. A (16.5%) are abundant. *Zeilleria rehmanni* (9.9%), *Gibbirhynchia moghrabiensis* (6.9%), *Prionorhynchia* sp. (5.4%), and *Squamirhynchia* sp. B (3.5%) are less common. Epibyssate (4.2%), cementing (1.1%) and endobyssate filibranchs (0.3%) are rare. This group occurs in bioclastic floatstones, bioclastic packstones, and floatstones with coated sponges in units 3 and 5. They correspond to habitats above and below NSWB.

(6) The *Liospiriferina* sample group is represented by two samples with 512 individuals. Its sample-level richness (S) ranges between 8 and 10 species, the evenness (PIE) is between 0.47 and 0.71. This group is dominated by *Liospiriferina rostrata* (56.6%), *Nanogyra nana* (15.3%) and *Atreta intusstriata* (14.9%). *Gibbirhynchia moghrabiensis* (5.8%), *Squamirhynchia* sp. A (2.5%) and *Gibbirhynchia* sp. A (1.8%) are less common. Epibyssate filibranchs (*Plagiostoma* aff. *punctatum*, *Pseudolimea* sp.) are rare (1.3%). This group is limited to bioclastic packstones and floatstones with complex internal stratification and nested/stacked disarticulated bioclasts (i.e., habitats above NSWB) in Unit 3 (Fig. 5E).

(7) The *Zeilleria rehmanni* sample group is defined on the basis of seven samples with 1022 individuals. The sample-level richness (S) varies between 7 and 10 species, the evenness (PIE) is uniformly high (0.72-0.82). The sample group is dominated by *Zeilleria rehmanni* (36.4%), *Liospiriferina rostrata* (18.4%), and *Squamirhynchia* sp. A (18%). *Moorellina* sp. (6.6%), *Nanogyra nana* (5.9%) and *Atreta* sp. (3.8%) are less common. Epibyssate filibranchs are represented mainly by *Oxytoma* sp. (3.4%). This sample group occurs mainly in micrite-rich oncoidal floatstones (Fig. 5B-C) with abundant microbial coatings and coated sponges (i.e., habitats below MSWB), and less commonly in bioclastic floatstones (i.e., habitats below NSWB). It is typical of units 4-6.

(8) The *Zeilleria rehmanni – Oxytoma* sample group is represented by seven samples with 713 individuals. The sample-level richness (S) is between 6 and 10 species, the evenness (PIE) is moderately high (0.59-0.82). In addition to *Zeilleria rehmanni*, the epibyssate bivalve *Oxytoma* sp. dominates in terms of its numerical abundance (40.3%). However, this species is mainly represented by juveniles or subadults reaching 1-2 mm in size. *Nanogyra nana* (5.9%), *Liospiriferina rostrata* (6.4%), *Prionorhynchia* sp. (5%), *Discinisca* sp. (4.2%), and *Squamirhynchia* sp. A (4%) are less common. Cementing brachiopods (1.8%) and the cementing filibranch *Atreta* sp. (0.1%) are rare. They occur in bioclastic floatstones and in the brachiopod shell bed (Fig. 5F) that correspond to habitats below NSWB and MSWB, respectively. One sample is derived from crinoidal packstone, indicating habitat above NSWB. Sponges and thick microbial coatings are rare. The sample group is limited to units 4-6.

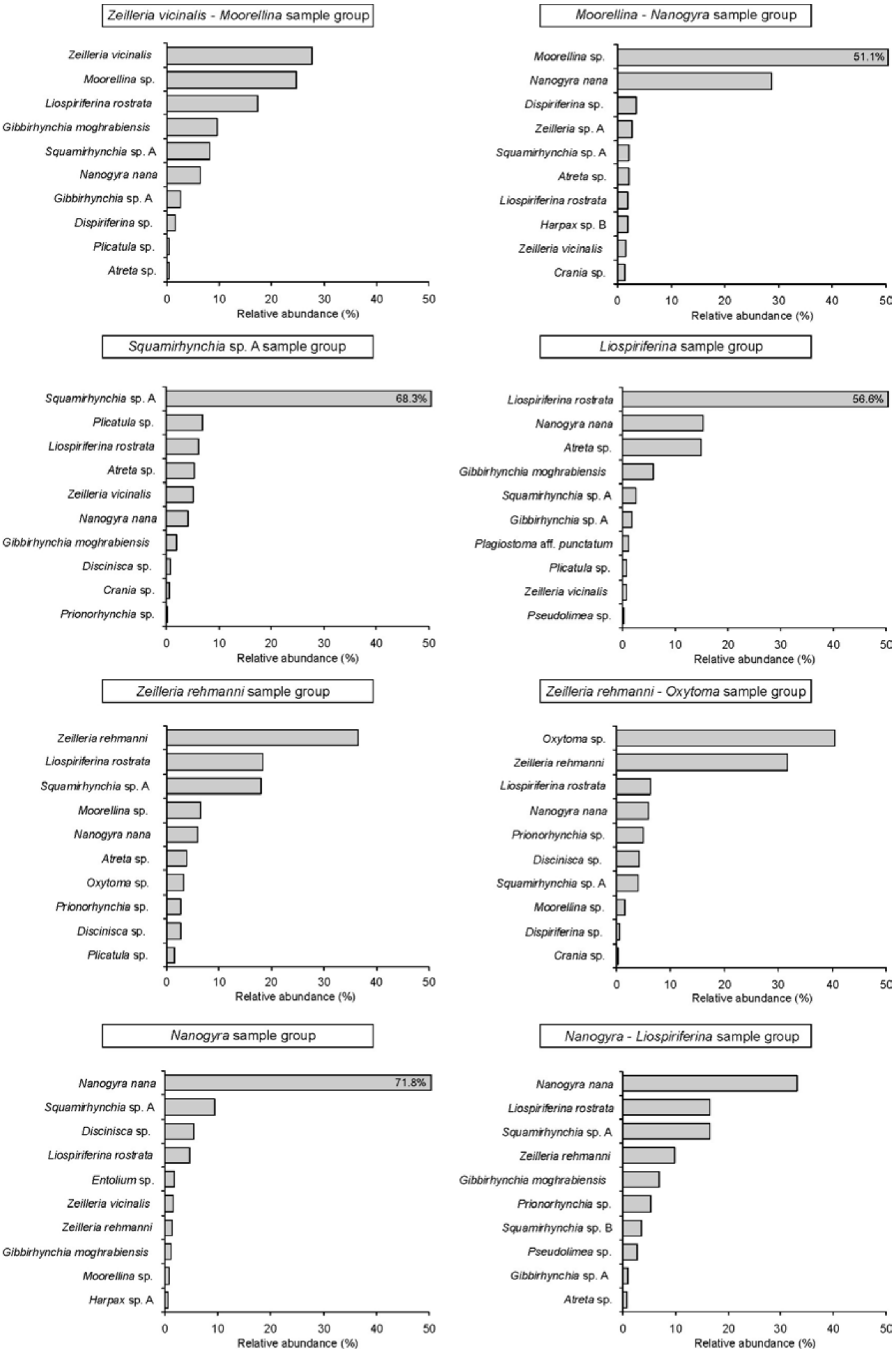


Figure 3 – Relative abundances of the ten most common taxa in eight sample groups of the lower member of the Foum Zidet Formation. The abundances are based on the complete dataset (all sieves).

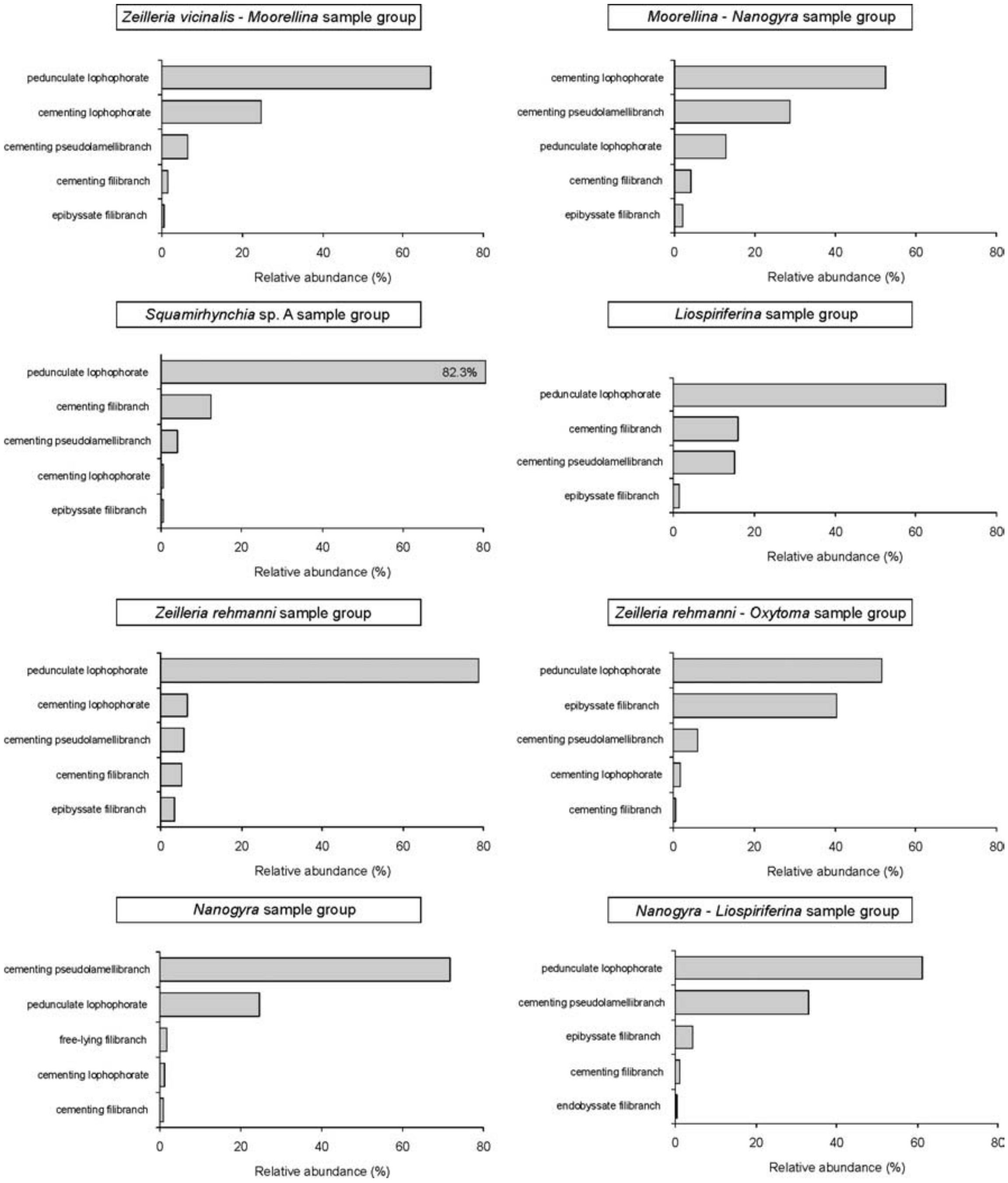


Figure 4 – Relative abundances of brachiopod and bivalve guilds in eight sample groups of the lower member of the Foum Zidet Formation. The abundances are based on the complete dataset (all sieves). Note that the sample groups are mainly dominated either by pedunculate brachiopods or cementing pseudolamellibranchs.

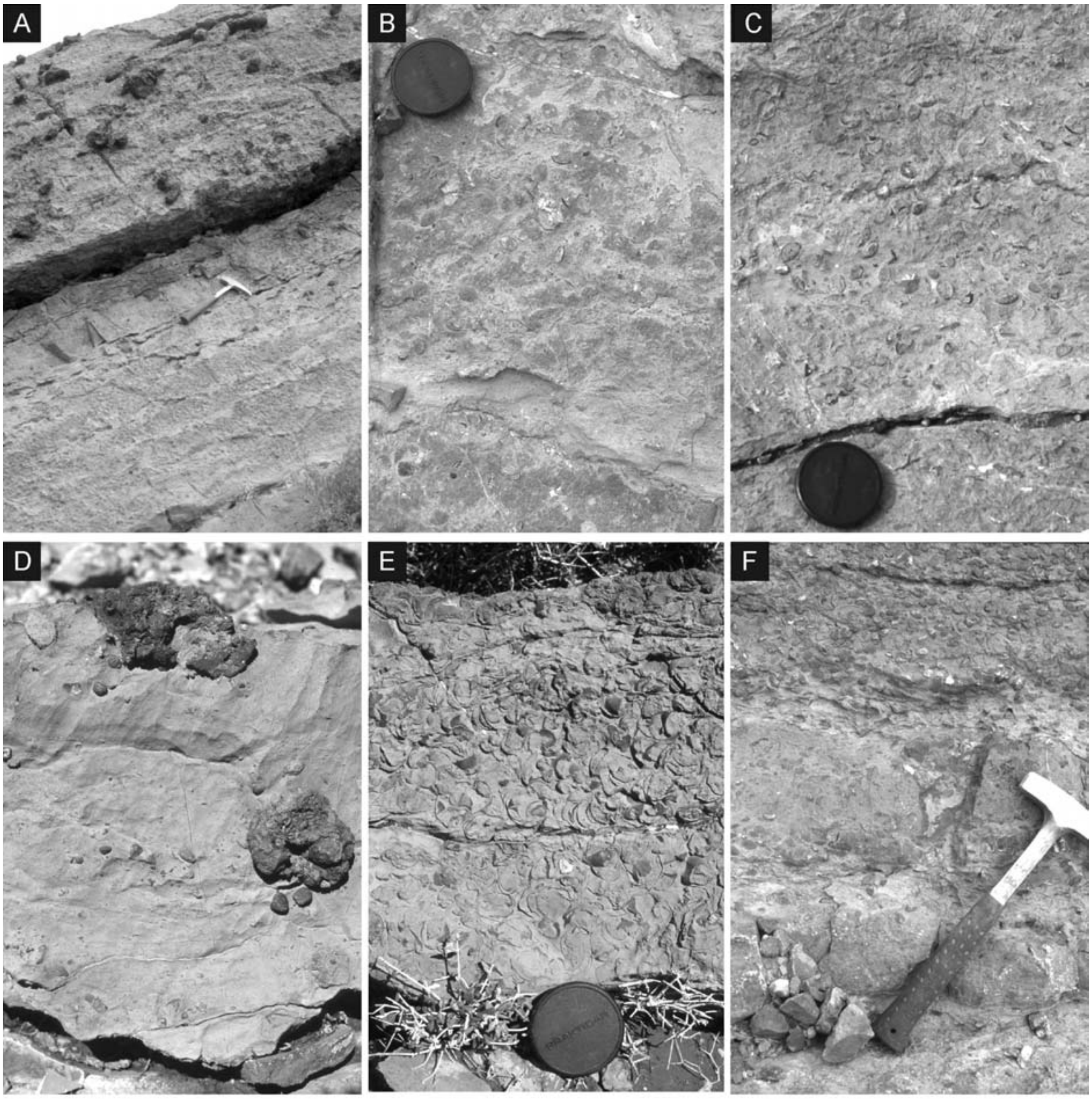


Figure 5 – Cross-sectional views of deposits with brachiopods and bivalves. A. Oncoidal floatstones (beds 6-7 in section FZ1) and sponge floatstones (bed 8) with the *Zeilleria vicinalis-Moorellina* sample group. B. Oncoidal floatstones with dispersed brachiopods (*Zeilleria rehmanni* sample group). Microbial crusts locally coalesce into boundstone. C. Oncoidal floatstone with articulated brachiopod shells (*Zeilleria rehmanni*) that are coated with microbial crusts. D. Sponge floatstone with the rhynchonellid *Squamirhynchia* that typically occurs in close vicinity of sponges. The diameter of the lower sponge is about 5 cm. E. Bioclastic packstone with nested, stacked and edgewise-oriented disarticulated valves of *Liospiriferina rostrata*. F. Bioclastic floatstone in the lower part is replaced by the brachiopod shell bed in the upper part. Both beds contain the *Zeilleria rehmanni-Oxytoma* sample group. Lens cap (5 cm) for scale.

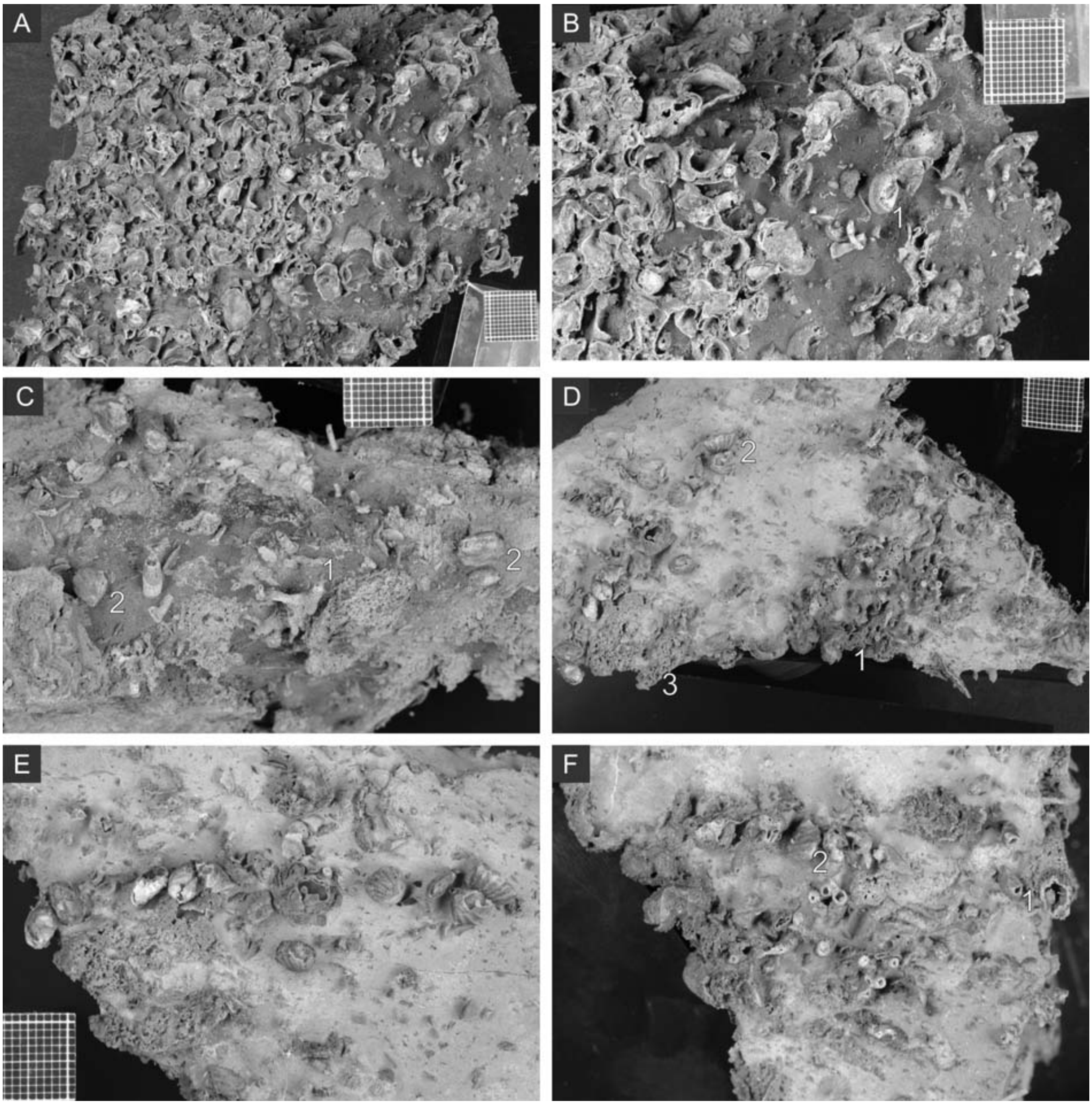


Figure 6 – A. Bedding plane view of a 1 cm-thick aggregate with *Nanogyra nana. Nanogyra* is cemented to hexactinellid sponges. B. Detail of Figure 6A. *Zeilleria* (1) occurs in areas with lower packing density of *Nanogyra*. C. Sponge floatstone with chaetetids (1), hexactinellids, and dispersed *Squamirhynchia* (2). D. Sponge floatstone with chaetetids (1) and hexactinellids (3). *Squamirhynchia* (2) forms clumps attached to the hexactinellid sponge. E. Detail of Figure 6D showing the clump with *Squamirhynchia*. F. Detail of Figure 6D showing dispersed shells of *Zeilleria vicinalis* (1) and *Squamirhynchia* (2) among branches of chaetetids.

Compositional differences among brachiopod- and bivalve-dominated samples

Species and genus abundance. In Q-mode NMDS based on species abundances (Fig. 7A), the *Squamirhynchia* sp. A sample group is compositionally replaced by the sample groups dominated by *Z. rehmanni* and *Z. vicinalis*, which pass into mixed brachiopod-bivalve sample groups and the *Nanogyra* sample group. In DCA (not shown), the samples dominated by *Z. rehmanni* have the most negative sample scores and samples dominated by *Z. vicinalis* have the most positive sample scores along the first axis. The maximum sample score along the first DCA axis is 3.4, implying the gradient length of 3.4 SD units. The compositional segregation of the *Z. rehmanni* and *Z. vicinalis – Moorellina* sample groups in Q-mode NMDS and DCA based on species abundances thus reflects mainly the temporal replacement of the two *Zeilleria* species.

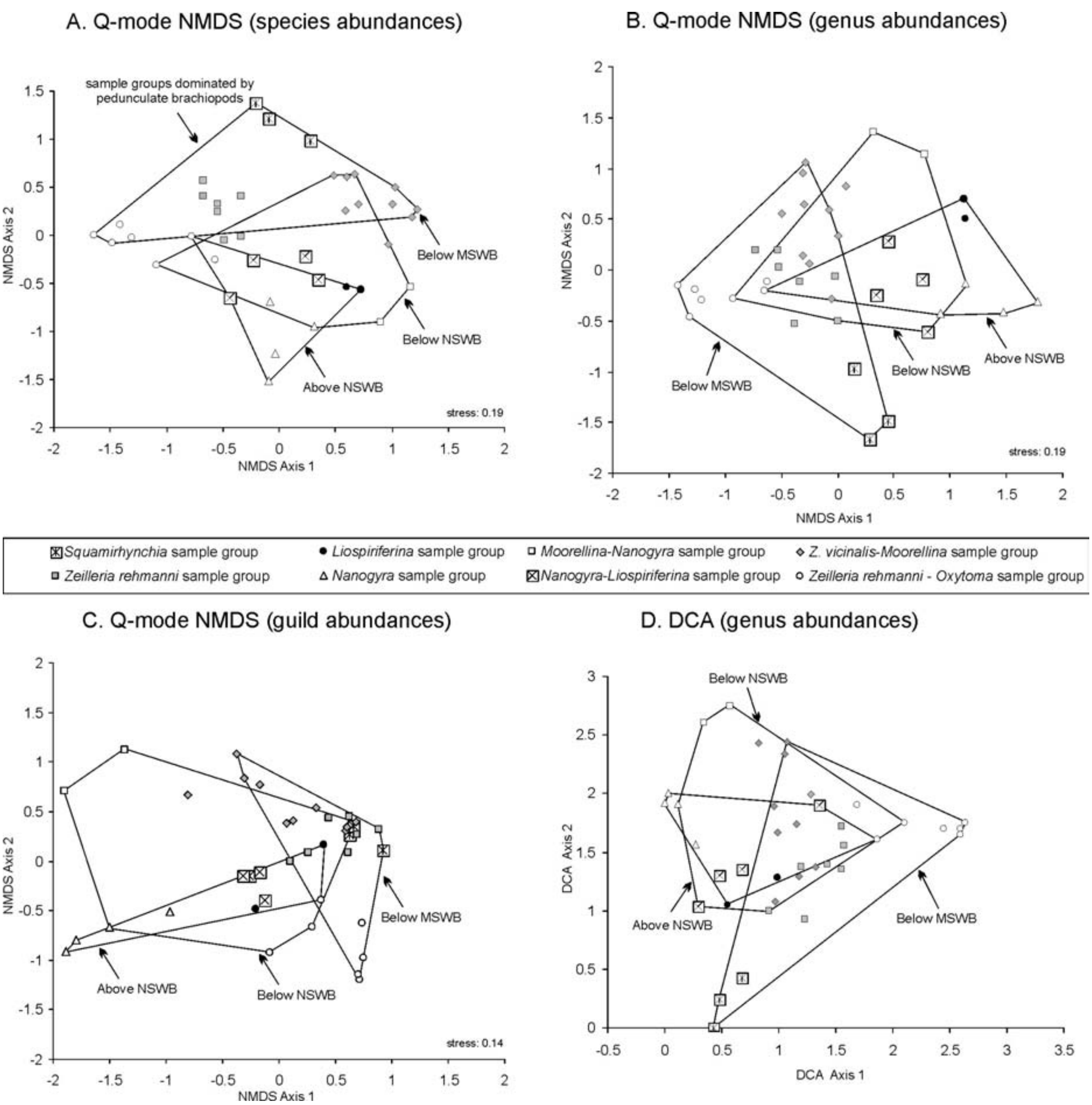


Figure 7 - Compositional relationship between samples and sample groups based on species, genus and guild abundances. The compositional segregation among three habitats is indicated by envelopes. The analyses are based on the complete dataset (all sieves). A. Q-mode non-metric multidimensional scaling (NMDS) of 39 samples based on species abundances. B. Q-mode NMDS of 39 samples based on genus abundances. C. Q-mode NMDS of 39 samples based on guild abundances. D. DCA of 39 samples based on abundances of genera.

In Q-mode NMDS based on abundances of genera, samples dominated by *Zeilleria* are compositionally segregated from samples dominated by *Liospiriferina, Squamirhynchia,* and *Nanogyra* (Fig. 7B). The mixed sample group with the bivalve *Oxytoma* is more similar to samples with *Zeilleria* than to other bivalve-dominated samples. In DCA based on abundances of genera (Fig.

7D), samples dominated by the oyster *Nanogyra* are compositionally replaced by brachiopod-dominated samples along the first axis, with the mixed *Z. rehmanni-Oxytoma* sample group occupying the most positive sample scores. The samples dominated by bivalves and brachiopods are thus not compositionally segregated in Q-mode NMDS and DCA based on abundances of genera. However, compositional sample-level differences can be seen between samples dominated by brachiopods and epibyssate bivalves on one hand and samples dominated by oysters on the other. In NMDS based on abundances of bivalve species only (not shown), there is no visible compositional segregation between brachiopod- and bivalve-dominated samples. The length of the compositional gradient along the first DCA axis is 2.6 SD units. This gradient length is equivalent to that based on species abundances evaluated separately for units 1-3 (2.5 SD units) and units 4-6 (2.6 SD units). This shows that the end-member samples from opposite sides of the compositional gradient shared some taxa in common and between-habitat (beta) diversity was thus relatively low.

Guild abundance. In Q-mode NMDS based on guild abundances (Fig. 7C), brachiopod and bivalve sample groups substantially overlap. With increasing sample scores along the first DCA axis, samples dominated by epibyssate bivalves are replaced by samples dominated by pedunculate brachiopods, which finally pass into samples dominated by cementing bivalves (not shown). Similarly as in Q-mode based on abundances of bivalve species, Q-mode NMDS based on abundance of bivalve guilds alone does not indicate differential abundance of bivalve guilds among brachiopod and bivalve samples. Therefore, sample-level differences based on guild abundances show that epifaunal communities dominated by brachiopods and bivalves do not consistently differ in terms of their guild composition.

R-mode based one-way ANOSIM	R	p-value	Number of permutations	Number of permuted R≥observed R
Brachiopod vs. bivalve species				
Complete dataset (all sieves)	-0.038	0.805	10000	8054
Restrictive dataset (specimens above 5 mm)	0.011	0.354	10000	3537
Guilds (species with more than three guilds)				
Complete dataset (all sieves)	-0.081	0.954	10000	9535
Restrictive dataset (specimens above 5 mm)	-0.054	0.8	10000	8004
Feeding strategies				
Complete dataset (all sieves)	-0.051	0.729	10000	7289
Restrictive dataset (specimens above 5 mm)	0.063	0.26	10000	2601

Table 1 – R-mode based analysis of similarities (ANOSIM) showing poor differences in abundance patterns between (1) brachiopod and bivalve species, (2) among guilds, and (3) among guilds subdivided according to their gill type.

Co-occurrence patterns of brachiopods and bivalves

Brachiopod and bivalve genera and guilds. R-mode NMDS based on abundances of species and genera demonstrate a strong overlap in bivalve and brachiopod abundances (Fig. 8A). A low or even negative and insignificant R values indicate that there are no differences among species abundances of brachiopods and bivalves (Tab. 1) Similarly, DCA based on species abundances does not show any consistent separation between brachiopods and bivalves, or among bivalve and brachiopod guilds (Fig. 8B).

R-mode NMDS based on guild abundances (Fig. 8C) and Bray-Curtis similarities indicate that pedunculate brachiopods co-occur commonly with cementing pseudolamellibranchs, cementing filibranchs, cementing brachiopods, and epibyssate filibranchs, and less commonly with rare endobyssate and free-lying filibranchs. To test the differences among species abundances between guilds, R-mode based ANOSIM tests the differences (1) among three guilds with more than three species (i.e., cementing filibranchs, epibyssate filibranchs and pedunculate brachiopods), and (2) among three guilds with distinct feeding strategies (i.e., brachiopods, filibranchs and pseudolamellibranchs). In both cases, the differences between the guilds are low or negative for the complete and restrictive datasets (Tab. 1). There are thus no consistent differences in abundance patterns between epifaunal bivalves and brachiopods.

DCA based on guild abundances (Fig. 8D) shows that along the first axis, epibyssate filibranchs occupying the most negative guild scores are replaced by pedunculate brachiopods and cementing filibranchs, cementing brachiopods and endobyssate filibranchs. Cementing pseudolamellibranchs and free-lying filibranchs occupy the most positive guild scores.

Brachiopod and bivalve species in units 1-3 and 4-6. To explore abundance patterns of bivalves and brachiopods larger than 5 mm on species level, the lower and upper parts of the lower member of the Foum Zidet Formation (i.e., units 1-3 and units 4-6) are evaluated separately. It follows that in terms of the most abundant taxa, *Zeilleria* and *Nanogyra* represent opposite parts of the gradient in abundance similarity, with *Liospiriferina* occupying an intermediate position.

In the lower part of the Foum Zidet Formation (units 1-3), *Nanogyra nana* co-occurs mainly with *Gibbirhynchia moghrabiensis* (Bray-Curtis similarity [BC] = 35) and *Liospiriferina rostrata* (BC = 31), less commonly with *Squamirhynchia* sp. A (BC = 27) and rarely with *Zeilleria vicinalis* (BC = 18). *Liospiriferina* closely co-occurs with *G. moghrabiensis* (BC = 47) and *Z. vicinalis* (BC = 47), and less commonly with *Squamirhynchia* sp. A (BC = 29). *Squamirhynchia* sp. A shows a relatively low Bray-Curtis similarity with *G. moghrabiensis* (BC = 30) and *Z. vicinalis* (BC = 29). In DCA based on species abundances in mesh size > 5 mm, the replacement of the dominant genera is related to their arrangement along the first axis (Fig. 9C). Along the first DCA axis, *Squamirhynchia* sp. A and *Zeilleria vicinalis* occupy the most negative scores. *Nanogyra nana* occupies the most positive species score. *Liospiriferina rostrata* and *Gibbirhynchia moghrabiensis* are characterized by intermediate scores.

In the upper part of the Foum Zidet Formation (units 4-6), *Nanogyra nana* shows the highest similarity in abundance patterns with *Squamirhynchia* sp. A (BC = 39) and *Liospiriferina rostrata* (BC = 26), and a low similarity with *Zeilleria rehmanni* (BC = 17). Brachiopods have more similar abundance patterns when compared to each other than with *Nanogyra*. *Liospiriferina rostrata* shows high Bray-Curtis similarities with *Squamirhynchia* sp. A (BC = 61) and *Zeilleria rehmanni* (BC = 47). *Squamirhynchia* sp. A has high Bray-Curtis similarity with *Zeilleria vicinalis* (BC = 47). Based on species abundances in mesh size > 5 mm, the most abundant species are ordered along the first DCA axis (Fig. 9D). With decreasing species scores, *Nanogyra nana* is replaced by *Squamirhynchia* sp. A, *Liospiriferina rostrata* and *Zeilleria rehmanni*.

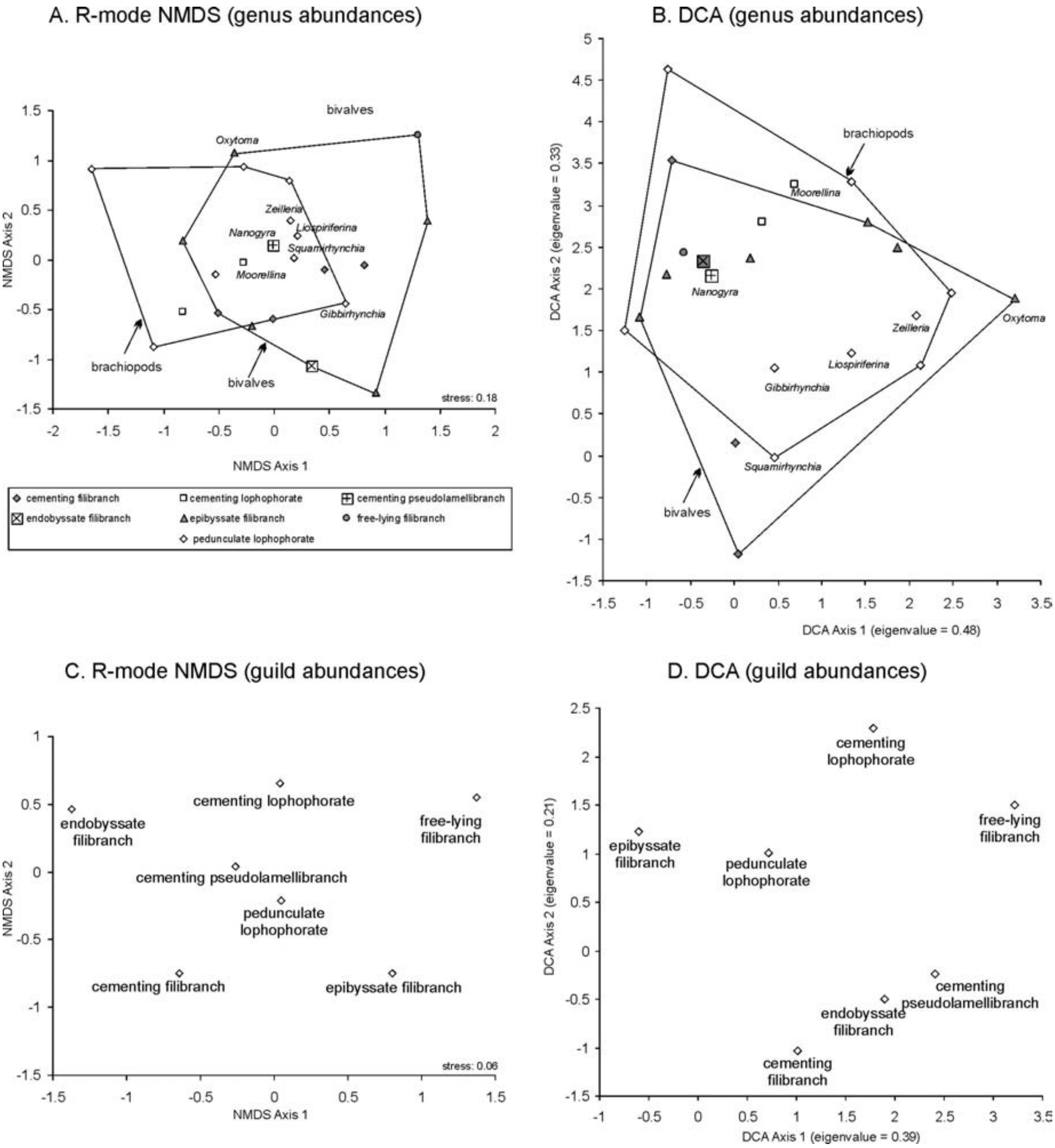


Figure 8 – Similarities in abundance patterns between brachiopods and bivalves based on abundances of genera and guilds. Genera are labeled according to their guild membership. The analyses show that there is no consistent difference in abundance patterns between brachiopods and bivalves. The analyses are based on the complete dataset (all sieves). A. R-mode non-metric multidimensional scaling (NMDS) of brachiopod and bivalve genera based on abundances of genera. B. DCA of brachiopod and bivalve genera based on genus abundances. C. Q-mode NMDS of brachiopod and bivalve guilds based on guild abundances. D. DCA of brachiopod and bivalve guilds based on guild abundances.

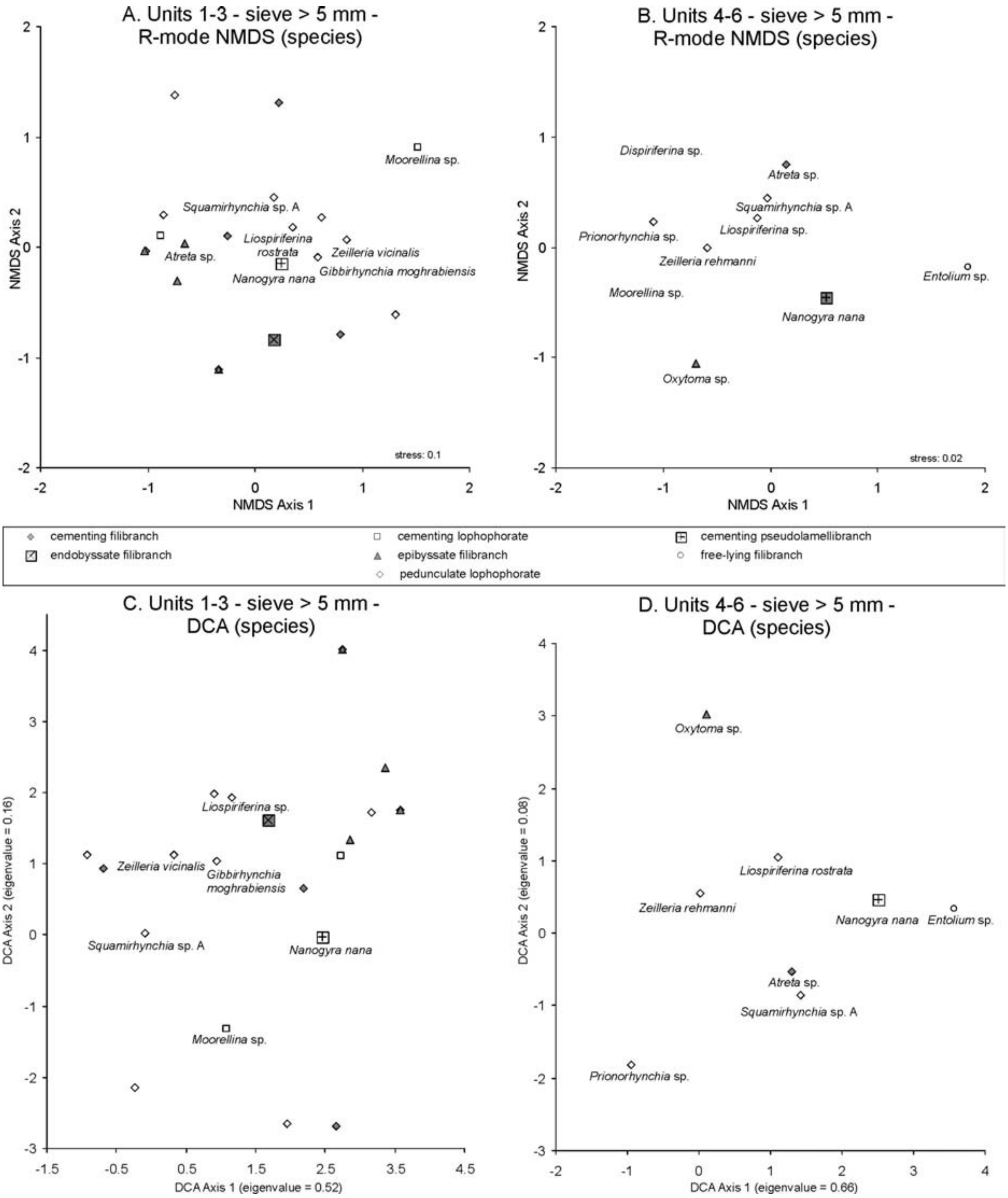
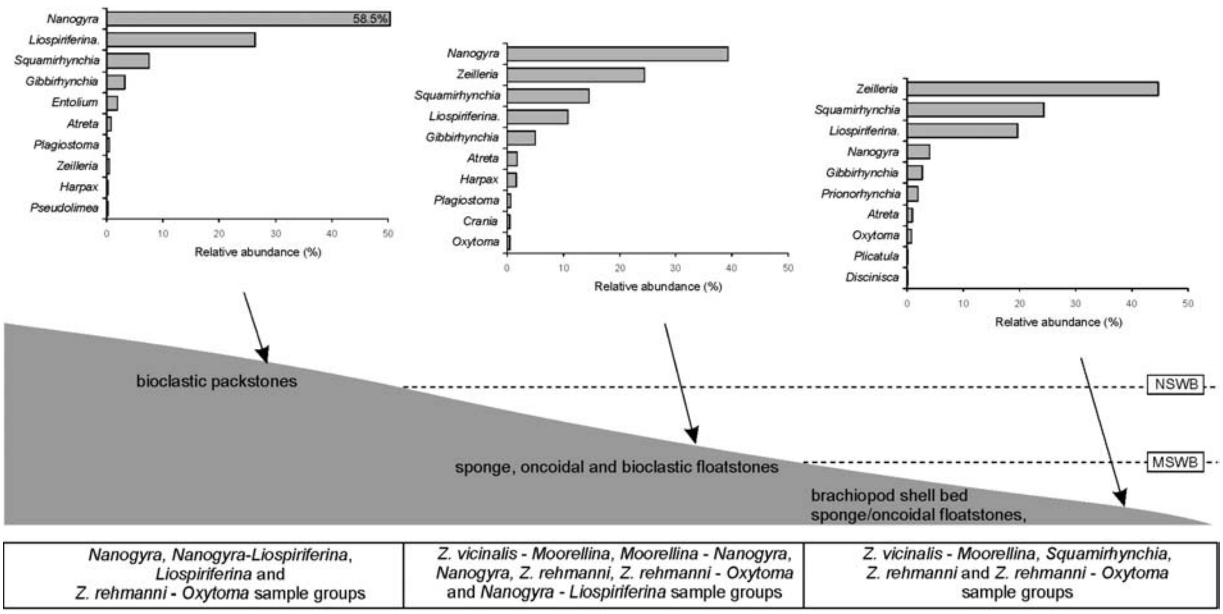


Figure 9 - - Similarities in abundance patterns of the most abundant brachiopods and bivalves based on species abundances (specimens > 5 mm). The lower and upper parts of the lower member are analysed separately. Species are labeled according to their guild membership. A. R-mode non-metric multidimensional scaling (NMDS) of brachiopod and bivalve species based on species abundances in units 1-3. B. R-mode NMDS of brachiopod and bivalve species based on species abundances in units 4-6. C. Detrended correspondence analysis (DCA) of brachiopod and bivalve species based on species abundances in units 1-3. D. DCA of brachiopod and bivalve species based on species abundances in units 4-6.

A. Genera - above 5 mm (Foum Zidet Formation)



B. Guilds - above 5 mm (Foum Zidet Formation)

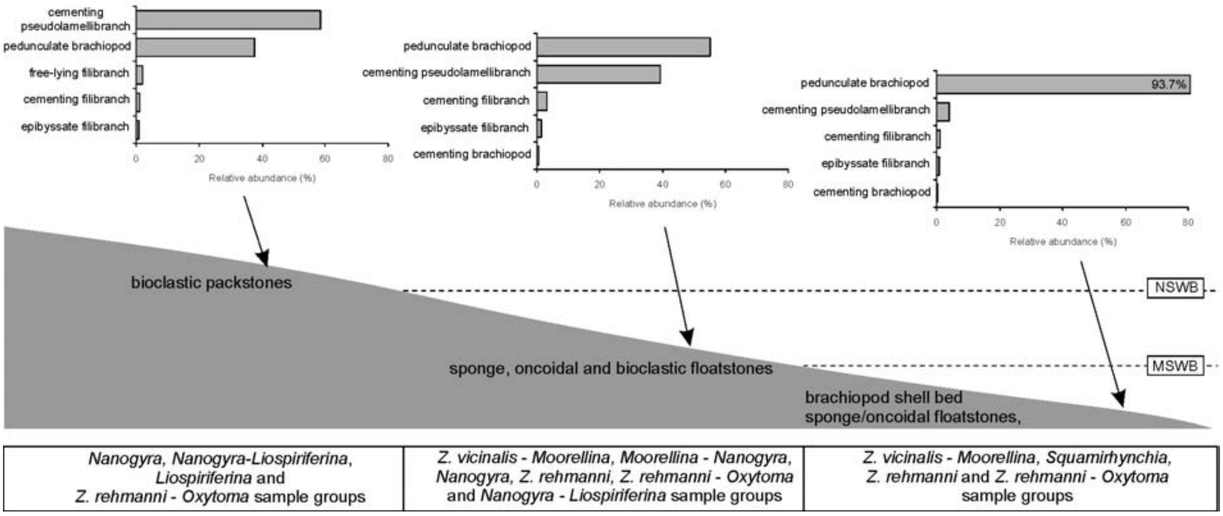


Figure 10 - Between-habitat differences in abundances of genera (A) and guilds (B). Pedunculate brachiopods increased and cementing pseudolamellibranchs decreased in abundance towards deeper habitats. The abundances are based on the dataset with specimens > 5 mm.

One-way ANOSIM-between-habitat differences	R	p-value (alpha = 0.05/3)	Number of permutations	Number of permuted R≥observed R
Genera - all sieves - habitats:				
Global test	0.224	0.0003	10000	3
below MSWB, below NSWB	0.105	0.043	10000	430
below NSWB, above NSWB	0.155	0.047	10000	468
below MSWB, above NSWB	0.466	0.0002	10000	2
Genera - > 5 mm - habitats:				
Global Test	0.358	0.0002	10000	2
below MSWB, below NSWB	0.257	0.002	10000	23
below NSWB, above NSWB	0.231	0.035	10000	352
below MSWB, above NSWB	0.652	0.0001	10000	1
Guilds - all sieves - habitats:				
Global Test	0.21	0.002	10000	19
below MSWB, below NSWB	0.168	0.01	10000	104
below NSWB, above NSWB	0	0.416	10000	4164
below MSWB, above NSWB	0.413	0.002	10000	16
Guilds - > 5 mm - habitats:				
Global Test	0.503	<0.0001	10000	0
below NSWB, below MSWB	0.46	<0.0001	10000	0
below NSWB, above NSWB	0.001	0.382	10000	3821
below MSWB, above NSWB	0.82	<0.0001	10000	0

Table 2 – Q-mode based one-way analysis of similarities (ANOSIM) shows significant differences in genus and guild abundances among three habitats. Note: NSWB – normal storm wave base, MSWB – maximum storm wave base. The values in indicate significant results, the values in italics indicate results of borderline significance after the Bonferroni correction.

Compositional differences among habitats

The differences in sample-level composition among habitats above NSWB, below NSWB and below MSWB are significant both for genus and guild abundances, regardless of the analysed mesh size (one-way ANOSIM). The results of pairwise between-habitat comparisons partly depend on the mesh size. The differences between habitats above NSWB and below MSWB are consistently significant or of borderline significance both for genus and guild abundances (Tab. 2). The difference between habitats above NSWB and below NSWB is of borderline significance for genus abundances, and insignificant for guild abundances (Tab. 2). The compositional differences among three habitats are also visualized in Q-mode NMDS (Fig. 7A-C).

Analytical exclusion of specimens smaller than 5 mm changes the relative abundances of taxa and guilds. It affects small-sized genera (*Moorellina, Discinisca*) and genera with abundant juveniles (*Oxytoma, Atreta, Plicatula*). The same effect causes that cementing brachiopods, and cementing and epibyssate filibranchs decrease in their abundance with exclusion of smaller mesh sizes. Rank abundances of other genera and guilds are mostly similar across different mesh sizes. Shallow habitats above NSWB were dominated by the cementing pseudolamellibranch *Nanogyra* and the pedunculate brachiopod *Liospiriferina*, with less common *Zeilleria, Squamirhynchia* and *Gibbirhynchia* (Fig. 10A). With increasing mesh size, *Nanogyra* increases in abundance and dominates when compared to all brachiopods. Habitats below NSWB were dominated by *Nanogyra* and *Zeilleria*, followed by *Squamirhynchia, Liospiriferina* and *Gibbirhynchia* (Fig. 10A). The cementing brachiopod *Moorellina* was the third most abundant genus when all sizes are analysed. In contrast to habitats above NSWB, pedunculate brachiopods were more common than cementing pseudolamellibranchs in all mesh sizes (Fig. 10B). *Zeilleria* and *Squamirhynchia* were dominant in deep habitats below MSWB, followed by less common *Liospiriferina* and rare *Nanogyra*. *Moorellina* and *Oxytoma* were also abundant when all mesh sizes are analysed. Deep habitats below MSWB were thus predominantly occupied by pedunculate brachiopods (Fig. 10B).

One-way ANOSIM-between-substrate differences	R	p-value (alpha = 0.05/3)	Number of permutations	Number of permuted R≥observed R
Genera - all sieves - substrate:				
Global test	0.209	0.0003	10000	3
microbial crusts vs. sponge colonies	0.303	0.0063	10000	63
microbial crusts vs. bioclastic debris	0.143	0.0052	10000	52
sponges vs. bioclastic debris	0.263	0.0052	10000	52
Genera - > 5 mm - substrate:				
Global test	0.198	0.0023	10000	23
microbial crusts vs. sponge colonies	0.475	<0.0001	10000	0
microbial crusts vs. bioclastic debris	0.032	0.2	10000	2009
sponges vs. bioclastic debris	0.199	0.025	10000	252
Guilds - all sieves - substrate:				
Global test	0.253	<0.0001	10000	0
microbial crusts vs. sponge colonies	0.33	0.0063	10000	63
microbial crusts vs. bioclastic debris	0.203	0.0012	10000	12
sponges vs. bioclastic debris	0.32	0.006	10000	60
Guilds - > 5 mm - substrate:				
Global test	0.204	0.0026	10000	26
microbial crusts vs. sponge colonies	0.504	0.0011	10000	11
microbial crusts vs. bioclastic debris	0.018	0.2314	10000	2314
sponges vs. bioclastic debris	0.227	0.025	10000	250

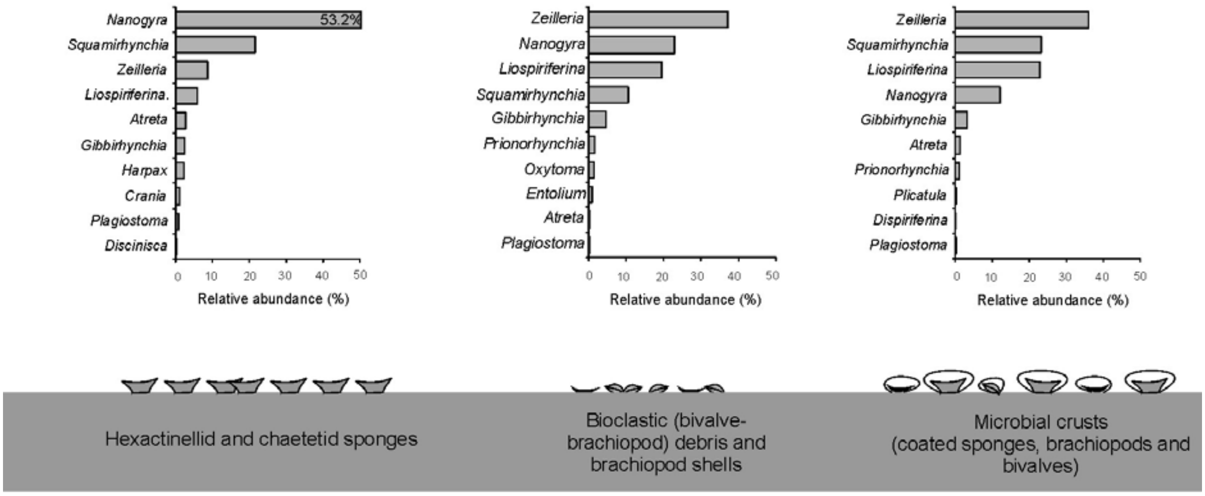
Table 3 - Q-mode based one-way analysis of similarities (ANOSIM) shows significant differences in genus and guild abundances among three substrates.

Compositional differences among substrates

Samples split into three substrates (i.e., sponges, microbial crusts, and bioclastic debris) significantly differ in genus and guild abundances (Tab. 3). Pairwise between-substrate comparisons indicate that differences between sponges and microbial crusts, and between sponges and bioclastic debris are significant or of borderline significance when all sizes are analysed. Analytical exclusion of smaller sizes decreases the difference in community composition between sponges and bioclastic debris (both in genus and guild analyses) (Tab. 3).

With exclusion of smaller specimens, (1) rank abundance of the epibyssate bivalve *Oxytoma* markedly decreased on substrates with bioclastic debris, (2) rank abundance of the cementing brachiopod *Moorellina* strongly decreased on substrates represented by sponges and microbial crusts, and (3) pedunculate brachiopods were replaced in the first rank by *Nanogyra* on sponge substrates owing to the exclusion of brachiopod juveniles. Analysing specimens > 5 mm, sponge substrates with chaetetid and siliceous sponges are dominated by *Nanogyra* and *Squamirhynchia*, followed by the less common pedunculate brachiopods *Zeilleria* and *Liospiriferina*. *Nanogyra* dominats over all other brachiopods (Fig. 11A). Microbial crusts are occupied by the pedunculate brachiopods *Zeilleria, Squamirhynchia*, and *Liospiriferina*, followed by the less common bivalve *Nanogyra* (Fig. 11A-B). *Zeilleria*, *Nanogyra,* and *Liospiriferina* are the most abundant genera on substrates formed by bioclastic debris.

A. Between-substrate differences in genus abundances (above 5 mm)



B. Between-substrate differences in guild abundances (above 5 mm)

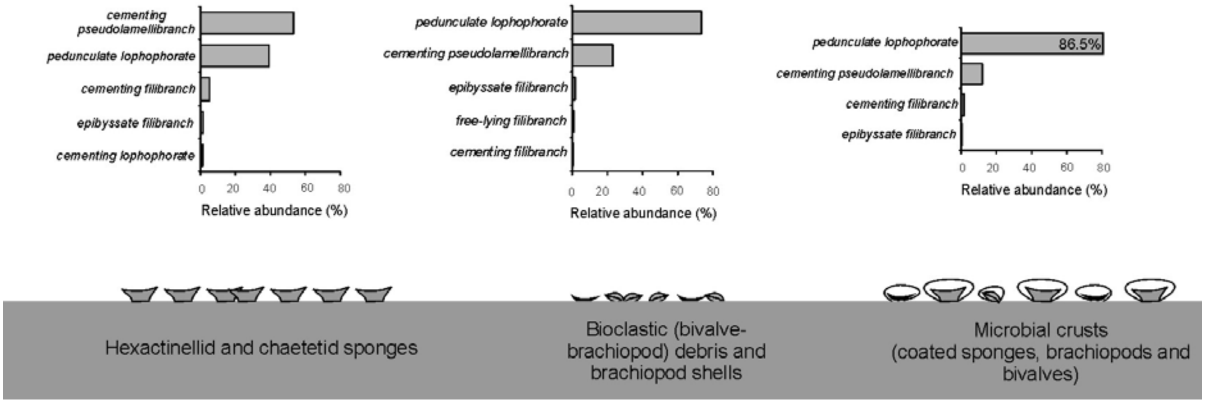


Figure 11 - Between-substrate differences in abundances of genera (A) and guilds (B). Cementing pseudolamellibranchs dominated on substrates formed by sponges, and pedunculate brachiopods dominated on microbial crusts. The abundances are based on the dataset with mesh size > 5 mm.

Separation of habitat and substrate effects

Although one-way analyses demonstrate that abundance of brachiopods and bivalves correlated with varying habitat and substrate gradients, two-way crossed analyses (Warwick et al., 1990; Warwick and Clarke, 1991; Clarke, 1993) test relationship between abundance patterns and one environmental factor (e.g., habitat) by removing the variation caused by another factor (e.g., substrate). In this case, the differences between habitats are tested within the same substrate type, and the differences between substrate types are tested within the same habitat. A global R statistic for the habitat test is an average of three R values which are calculated separately for three substrate types.

Allowing for the fact that there are substrate effects, two-way crossed ANOSIM shows that there are significant differences in composition among the three habitats. A relatively high R value and significant p-value follow from genus and guild abundances at all mesh sizes (Tab. 4). Pairwise comparisons between habitats below MSWB and below NSWB, and between habitats above NSWB and below MSWB are significant. The difference between habitats above and below NSWB is low and of borderline (genus level) or no significance (guild level). Allowing for the fact that there are habitat effects, two-way crossed ANOSIM demonstrates that there are significant differences in composition among the three substrate types at all mesh sizes (Tab. 4). Pairwise comparisons among three substrates are mostly significant both for genus and guild abundances. The difference between microbial crusts and sponges increases with decreasing mesh size. In contrast, the difference between microbial crusts and bioclastic debris decreases with decreasing mesh size (Tab. 4). Although substrates with microbial crusts did not occur above NSWB, two-way crossed ANOSIM thus demonstrates that *both* habitat and substrate had significant effects on the community composition.

Two-way ANOSIM - effects of habitat and substrate (restricted dataset > 5 mm)	R	p-value (alpha = 0.05/3)	Number of permutations	Number of permuted R≥observed R
Habitat effects, allowing for substrate effects				
Global test	0.497	<0.0001	10000	0
below MSWB, below NSWB	0.468	0.002	10000	15
below MSWB, above NSWB	0.968	0.002	504	1
below NSWB, above NSWB	0.437	0.025	630	16
Habitat effects, allowing for substrate effects				
Global test	0.399	0.001	10000	10
oncoids, sponge colonies	0.408	0.02	10000	198
oncoids, debris	0.24	0.06	10000	598
sponge colonies, debris	0.65	0.001	7350	8

Table 4 - Two-way analysis of similarities (ANOSIM) separating effects of habitat and substrate differences. Note *both* factors had significant effects on abundances of genera.

Two-way ANOSIM (temporal effects on genera > 5 mm, allowing for habitat effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Global test	0.214	0.027	10000	269

Two-way ANOSIM (habitat effects on genera > 5 mm, allowing for temporal effects)	R	p-value (alpha = 0.05/3)	Number of permutations	Number of permuted R≥observed R
Global test	0.558	0.0004	10000	4
Pairwise tests:				
below NSWB, below MSWB	0.42	0.009	10000	89
below NSWB, above NSWB	0.704	0.050	40	2
below MSWB, above NSWB	1	0.002	560	1

Two-way ANOSIM (temporal effects on genera > 5 mm, allowing for substrate effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Global test	0.243	0.018	10000	176

Two-way ANOSIM (substrate effects on genera > 5 mm, allowing for temporal effects)	R	p-value (alpha = 0.05/3)	Number of permutations	Number of permuted R≥observed R
Global test	0.343	0.006	10000	63
Pairwise tests:				
sponge colonies, oncoids	0.648	0.008	360	3
sponge colonies, debris	0.395	0.014	2568	22
oncoids, debris	0.335	0.027	10000	266

Table 5 - Two-way analysis of similarities (ANOSIM) separating (1) effects of habitat and time, and (2) effects of substrate and time. They show that *both* time and substrate/habitat factors had significant effects on genus abundances.

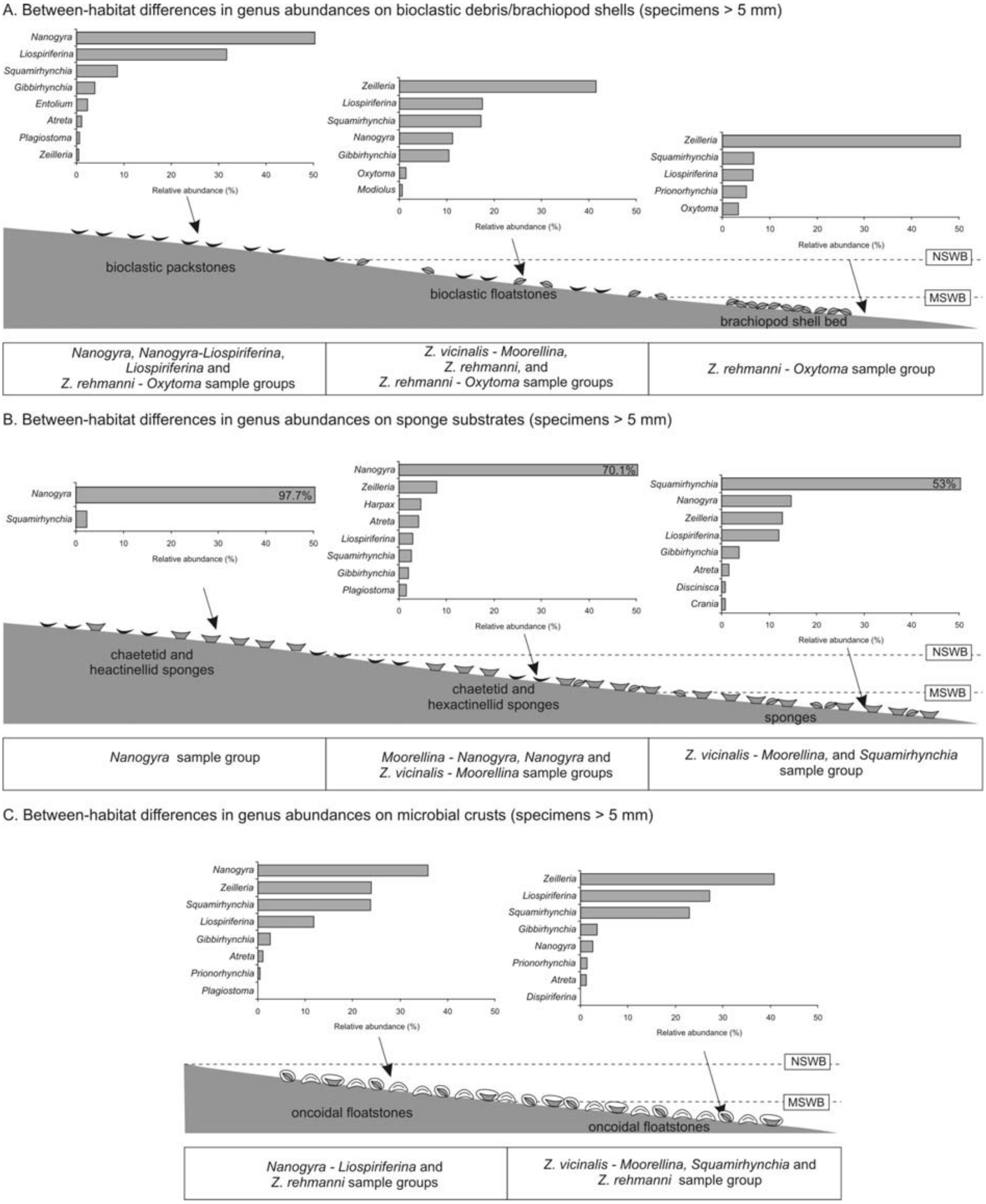


Figure 12 - Abundances of genera along a wave-base level transect with constant substrate type. A. Between-habitat differences on bioclastic substrates. B. Between-habitat differences on sponge substrates. C. Between-habitat differences on microbial crusts. The abundances are based on the dataset with mesh size > 5 mm.

In habitats with bioclastic debris and brachiopod shells, *Nanogyra* and *Liospiriferina* dominated in shallow habitats above NSWB (Fig. 12A). *Zeilleria, Liospiriferina* and *Squamirhynchia* dominated in habitats below NSWB. *Zeilleria* strongly dominated in deep habitats below MSWB. On sponge substrates, *Nanogyra* dominated in shallow habitats above and below NSWB (Fig. 12B). In deep habitats below MSWB, sponges were colonized by *Squamirhynchia*, followed by relatively common *Nanogyra*, *Zeilleria* and *Liospiriferina*. In habitats with microbial crusts, pedunculate brachiopods dominated both below NSWB and MSWB, accompanied by a decreasing abundance of cementing pseudolamellibranchs towards deeper habitats (Fig. 12C). *Nanogyra* was the most abundant genus in habitats below NSWB, followed by common *Zeilleria* and *Squamirhynchia*. *Zeilleria, Liospiriferina* and *Squamirhynchia* dominated on microbial crusts in deep habitats below MSWB.

It follows that within the same habitat, brachiopod and bivalve genera preferred different substrates, and on the same substrate, brachiopods and bivalves preferred different habitats. *Zeilleria* preferred microbial crusts and bioclasts, and *Squamirhynchia* dominated on sponge substrates in deep habitats below MSWB. Below NSWB, *Zeilleria* dominated on substrates formed by bioclasts, and *Nanogyra* dominated on substrates formed by sponges. *Nanogyra* dominated also on substrates formed by sponges and bioclasts in habitats above NSWB.

Separation of temporal and spatial effects

Two-way crossed ANOSIM evaluating temporal effects on community composition, allowing for habitat effects, demonstrates significant between-unit differences (R = 0.214, p = 0.027, Tab. 5). The main compositional turnover took place between sponge-dominated unit 3 and bioclast-dominated units 4-5 (R = 0.928, p = 0.001). Evaluating habitat effects on community composition but allowing for temporal effects, both global test and pairwise comparisons show significant compositional differences among the three habitats (Fig. 7). These results are in accord with one-way and two-way analyses of habitats effects.

Two-way crossed ANOSIM evaluating temporal effects on community composition but allowing for substrate effects also indicates significant between-unit differences (R = 0.243, p = 0.018, Tab. 5). Similarly as in the previous comparison, the substantial turnover took place between sponge-dominated unit 3 and bioclast-dominated units 4-5 (R = 0.397, p = 0.027). In addition, the difference between sponge-dominated units 2 and 3 is relatively high (R = 0.689, p = 0.006). Evaluating habitat effects on community composition but allowing for temporal effects, both global test and pairwise comparisons demonstrate significant compositional differences among the three substrates (Tab. 5).

It follows that equivalent habitats with respect to wave base level were dominated by different taxa and guilds at different times (Fig. 13). The temporal variations in abundance of the most common brachiopods and bivalves are summarized in time-environment diagrams in Figure 14. *Nanogyra* was consistently rare in habitats below MSWB and attained abundance peaks in shallow habitats above NSWB and below NSWB. *Zeilleria* dominated in habitats below MSWB with exception of the sponge-dominated unit 3 when this genus was rare in habitats below MSWB. In contrast, *Squamirhynchia* reached its abundance peak in habitats below MSWB in unit 3. *Liospiriferina* did not show consistent depth preferences because it dominated in habitats above NSWB in unit 3 and was more common in habitats below MSWB in other units. Environmental preferences of pedunculate brachiopods and cementing brachiopods in time-environment diagrams (Fig. 15) were relatively constant. The compositional turnover was thus mainly caused by varying habitat preferences among brachiopod genera, rather than by varying preferences between brachiopods and bivalves.

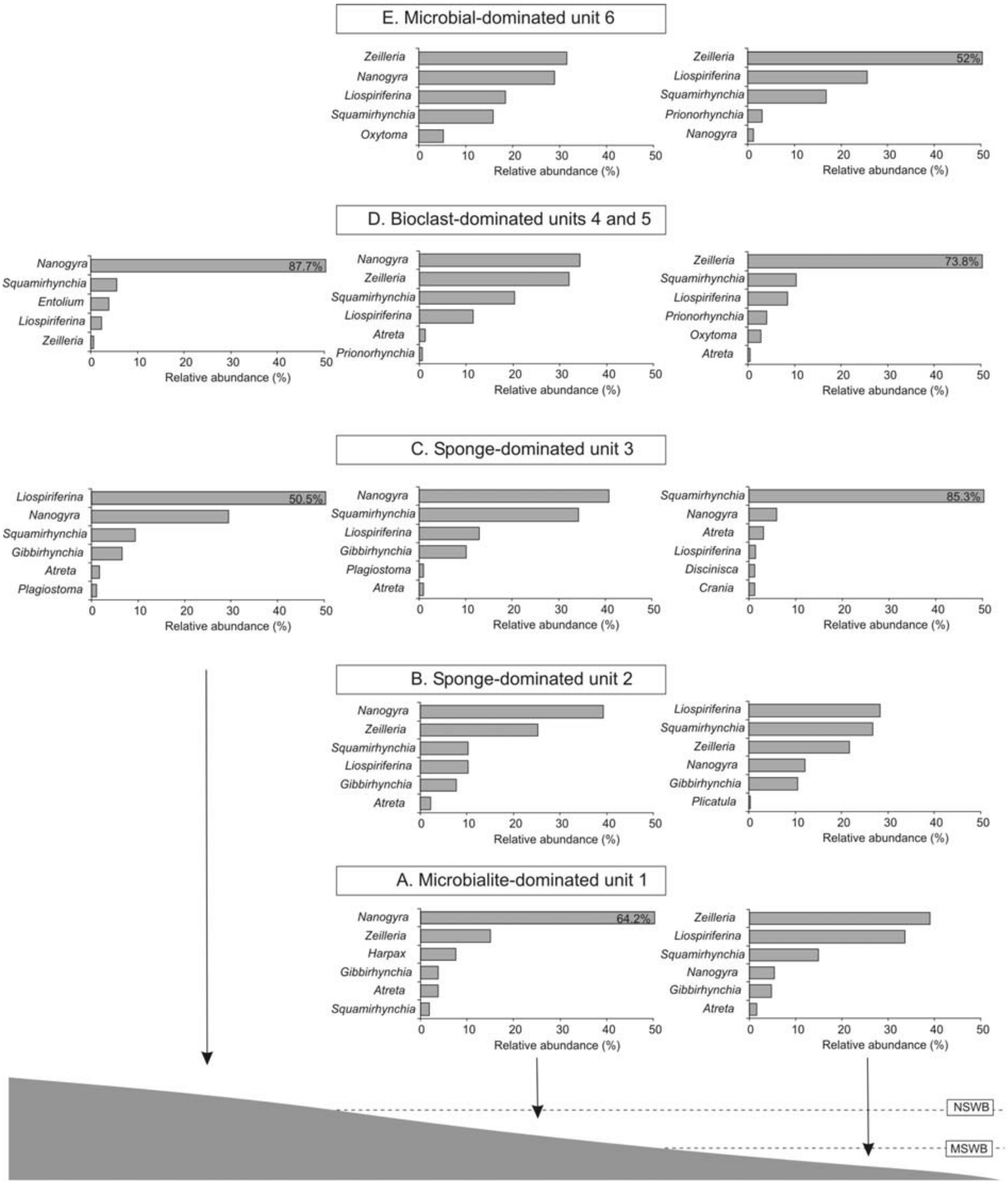
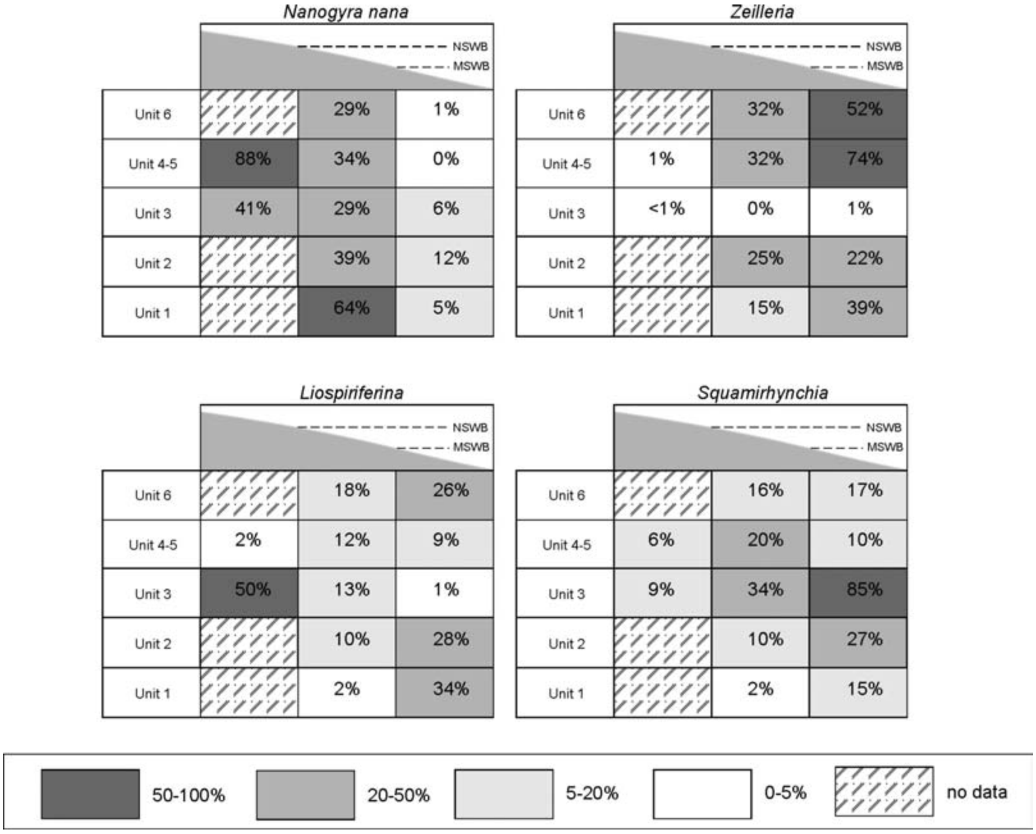


Figure 13 – Temporal variations in abundances of genera along the wave-base level transect within the lower member of the Foum Zidet Formation. A. Microbialite-dominated unit 1. B. Sponge-dominated unit 2. C. Sponge-dominated unit 3. D. Bioclast-dominated units 4-5. E. Microbialite-dominated unit 6. The abundances are based on the dataset with specimens > 5 mm.



Nanogyra nana			
Unit 6	▨	29%	1%
Unit 4-5	88%	34%	0%
Unit 3	41%	29%	6%
Unit 2	▨	39%	12%
Unit 1	▨	64%	5%

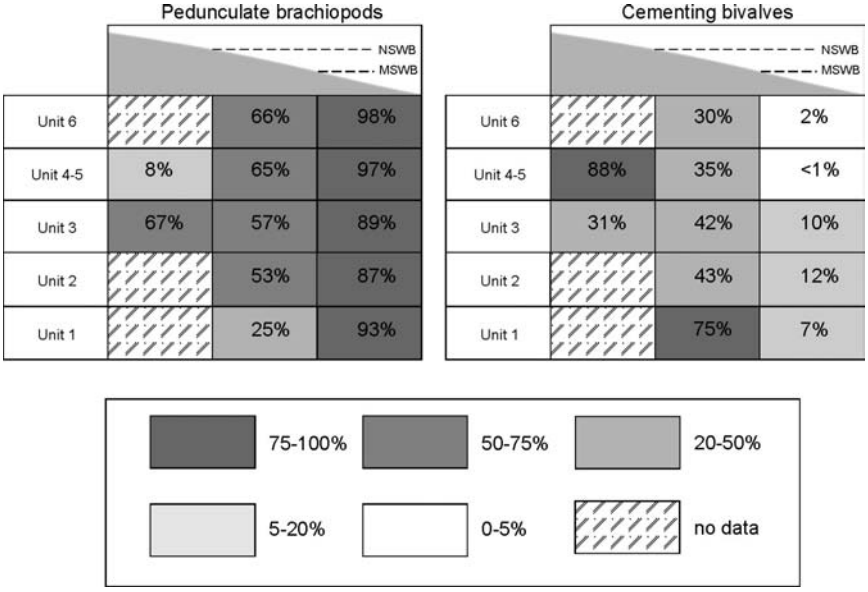
Zeilleria			
Unit 6	▨	32%	52%
Unit 4-5	1%	32%	74%
Unit 3	<1%	0%	1%
Unit 2	▨	25%	22%
Unit 1	▨	15%	39%

Liospiriferina			
Unit 6	▨	18%	26%
Unit 4-5	2%	12%	9%
Unit 3	50%	13%	1%
Unit 2	▨	10%	28%
Unit 1	▨	2%	34%

Squamirhynchia			
Unit 6	▨	16%	17%
Unit 4-5	6%	20%	10%
Unit 3	9%	34%	85%
Unit 2	▨	10%	27%
Unit 1	▨	2%	15%

50-100% 20-50% 5-20% 0-5% ▨ no data

Figure 14 – Time-environment diagrams of the oyster *Nanogyra* and the three most common brachiopod genera. Brachiopod genera vary in their habitat preferences in time. The abundances are based on the dataset with mesh size > 5 mm.



Pedunculate brachiopods			
Unit 6	▨	66%	98%
Unit 4-5	8%	65%	97%
Unit 3	67%	57%	89%
Unit 2	▨	53%	87%
Unit 1	▨	25%	93%

Cementing bivalves			
Unit 6	▨	30%	2%
Unit 4-5	88%	35%	<1%
Unit 3	31%	42%	10%
Unit 2	▨	43%	12%
Unit 1	▨	75%	7%

75-100% 50-75% 20-50%
5-20% 0-5% ▨ no data

Figure 15 – Time-environment diagrams of cementing bivalves (*Nanogyra, Atreta, Plicatula* and *Harpax)* and pedunculate brachiopods.

Survivorship analyses

Differences in population structure of four brachiopod and one bivalve species (i.e., *Zeilleria vicinalis, Zeilleria rehmanni, Liospiriferina rostrata*, *Squamirhynchia* sp. A, and *Nanogyra nana*) among substrates and among habitats are evaluated with size-frequency distributions (SFD), survivorship curves and size-specific mortality curves. They are summarized in terms of their median size, adult median size (> 5 mm), skewness and kurtosis in Table 6. Size-frequency distributions are shown in Figures 16-21. NMDS plots of five species are shown in Figure 22.

Between-substrate within-species comparisons. Zeilleria vicinalis assemblages are characterized by small median size and right-skewed SFDs on sponges (median = 4.3 mm) and microbial crusts (median = 5 mm) and mainly symmetrical SFDs with larger median size (7.7 mm) and adult median size (11.5 mm) on substrates formed by bioclastic debris (Fig. 16, Tab. 6). SFDs of assemblages from sponge substrates are leptokurtic (less peaked) than SFDs, in contrast to more peaked, platykurtic SFDs of assemblages from substrates formed by microbial crusts and bioclastic debris. Between-substrate differences in SFDs of *Zeilleria vicinalis* are significant using one-way ANOSIM (R = 0.34, p = 0.033, Tab. 7). SFDs of *Zeilleria rehmanni* from the brachiopod shell bed are invariably left-skewed (Fig. 17) and show a relatively high median size and adult median size (17 mm). In contrast, SFDs of *Zeilleria rehmanni* from substrates formed by microbial crusts are right-skewed and have a low median size (5.6 mm) and low adult median size (9.5 mm). Between-substrate differences in SFDs of *Zeilleria rehmanni* are high and highly significant using both one-way and two-way ANOSIM (Tab. 7). SFDs of *Liospiriferina rostrata* are right-skewed and have a relatively low median size on substrates formed by microbial crusts (median = 3.2 mm, adult median = 7.4 mm, Fig. 18) and sponges (median = 2.2 mm, adult median = 6.8 mm, Fig. 19). Assemblages from substrates formed by bioclastic debris are also right-skewed but have a higher median size (4.7 mm, Fig. 19). Adult median size (7.1 mm) does not differ from assemblages from sponges and microbial crusts. Between-substrate differences in SFDs of *Liospiriferina rostrata* are very low and insignificant using both one-way and two-way ANOSIM (Tab. 7). With an exception of one left-skewed SFD (FZ2-12.6), *Squamirhynchia* sp. A is invariably characterized by right-skewed SFDs (Fig. 20). The median size is also comparable between substrates formed by sponges (3.9 mm), microbial crusts (4.1 mm) and bioclastic debris (4.6 mm). In accord with these univariate results, between-substrate differences in SFDs of *Squamirhynchia* sp. A are low and insignificant using one-way ANOSIM (R = 0.23, p = 0.081, Tab. 7). *Nanogyra nana* is characterized by approximately symmetrical SFDs with a relatively high median size (8 mm) on sponge substrates (Fig. 21). In contrast, it is characterized by right-skewed SFDs with a relatively low median size on substrates with bioclastic debris (5.8 mm) and microbial crusts (5.6 mm). Similarly, assemblages from sponge substrates have higher adult median size (9.2 mm) than assemblages from substrates formed by microbial crusts (7.3 mm) and bioclasts (7.1 mm). Between-substrate differences in SFDs of *Nanogyra nana* are significant using both one-way and two-way ANOSIM (Tab. 7).

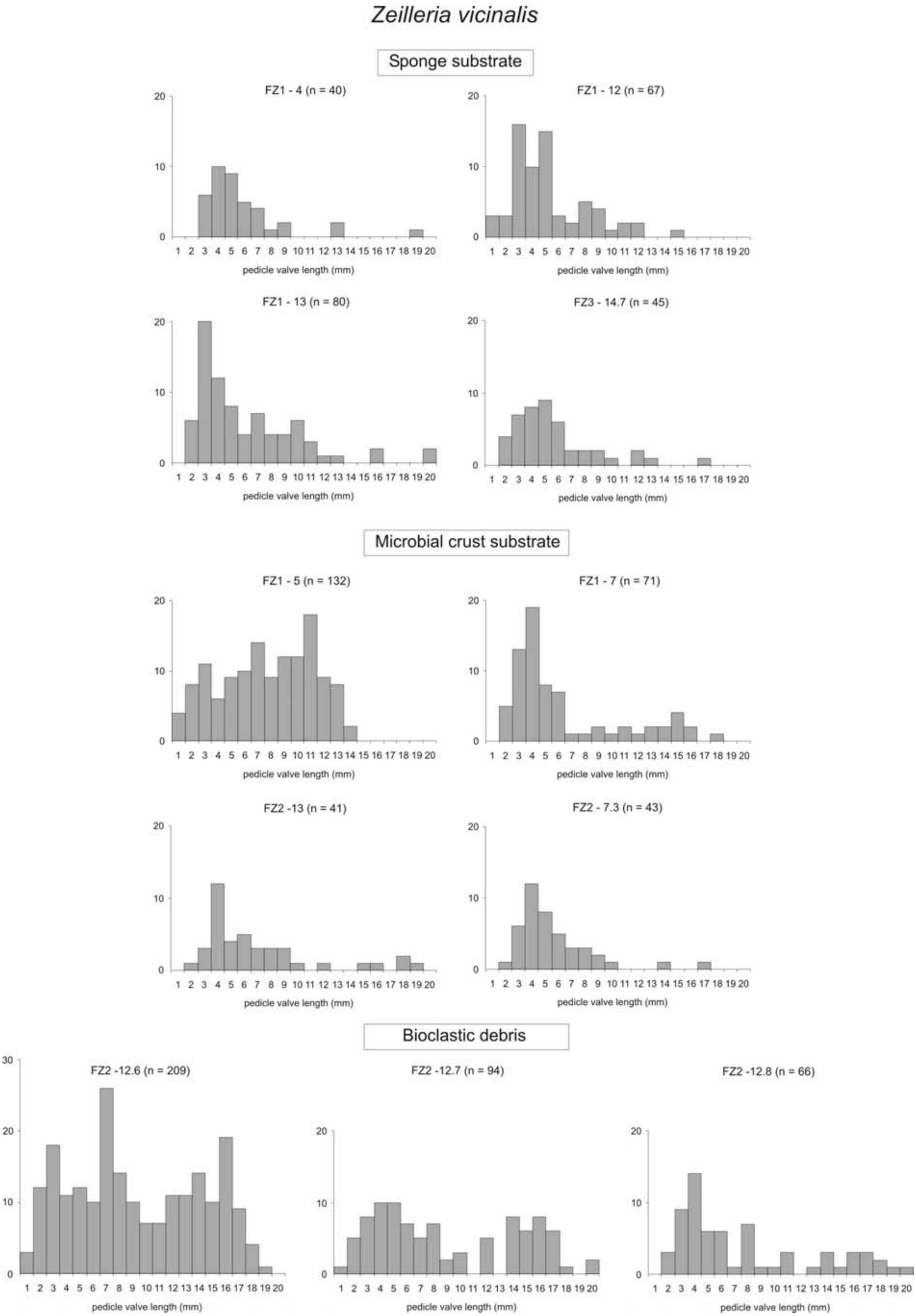


Figure 16 – Between-substrate differences in size-frequency distributions of *Zeilleria vicinalis*.

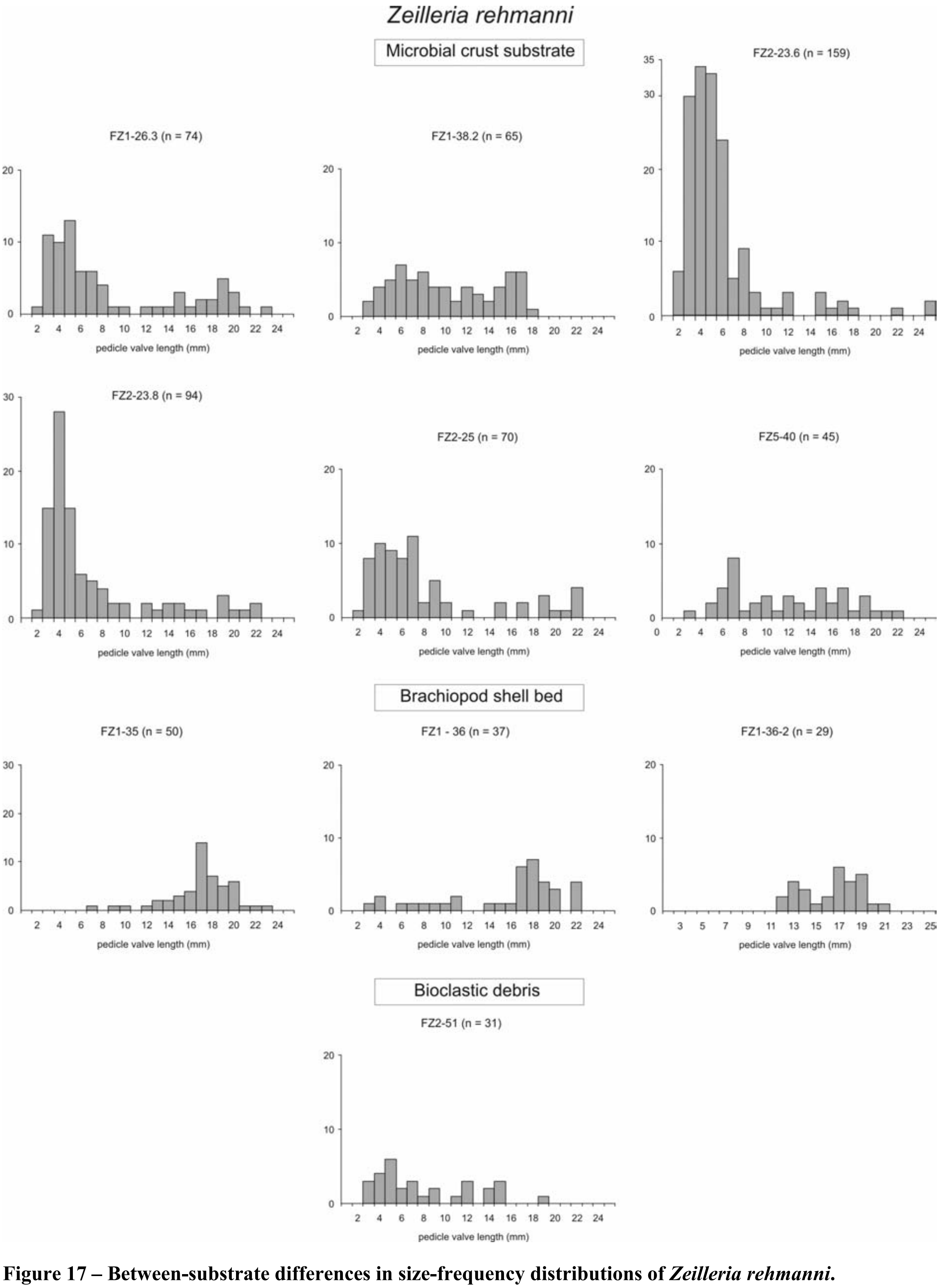


Figure 17 – Between-substrate differences in size-frequency distributions of *Zeilleria rehmanni*.

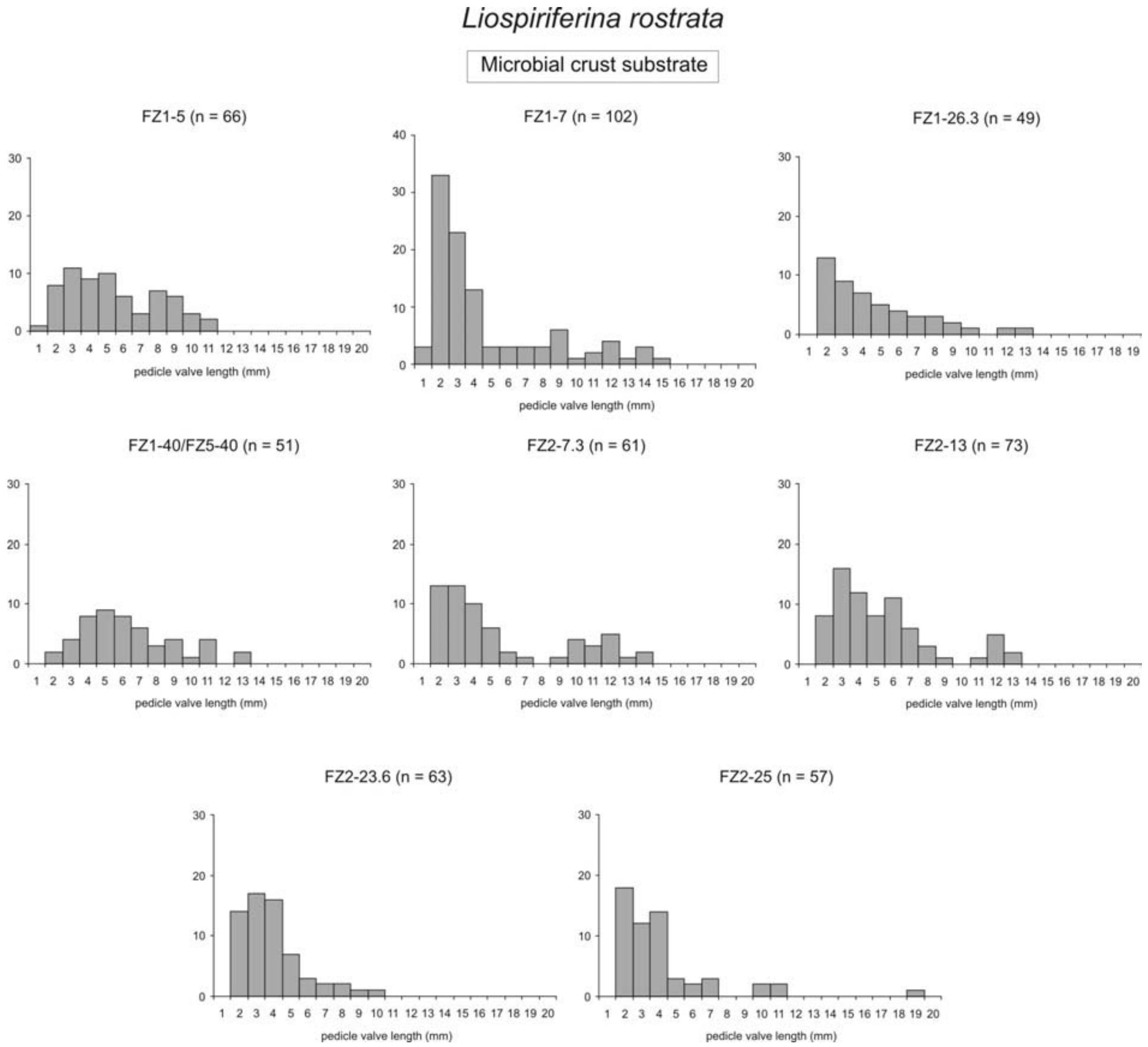


Figure 18 – Size-frequency distributions of *Liospiriferina rostrata* from substrates formed by microbial crusts. For comparison with assemblages from sponge substrates and bioclast-rich substrates, see Fig. 19.

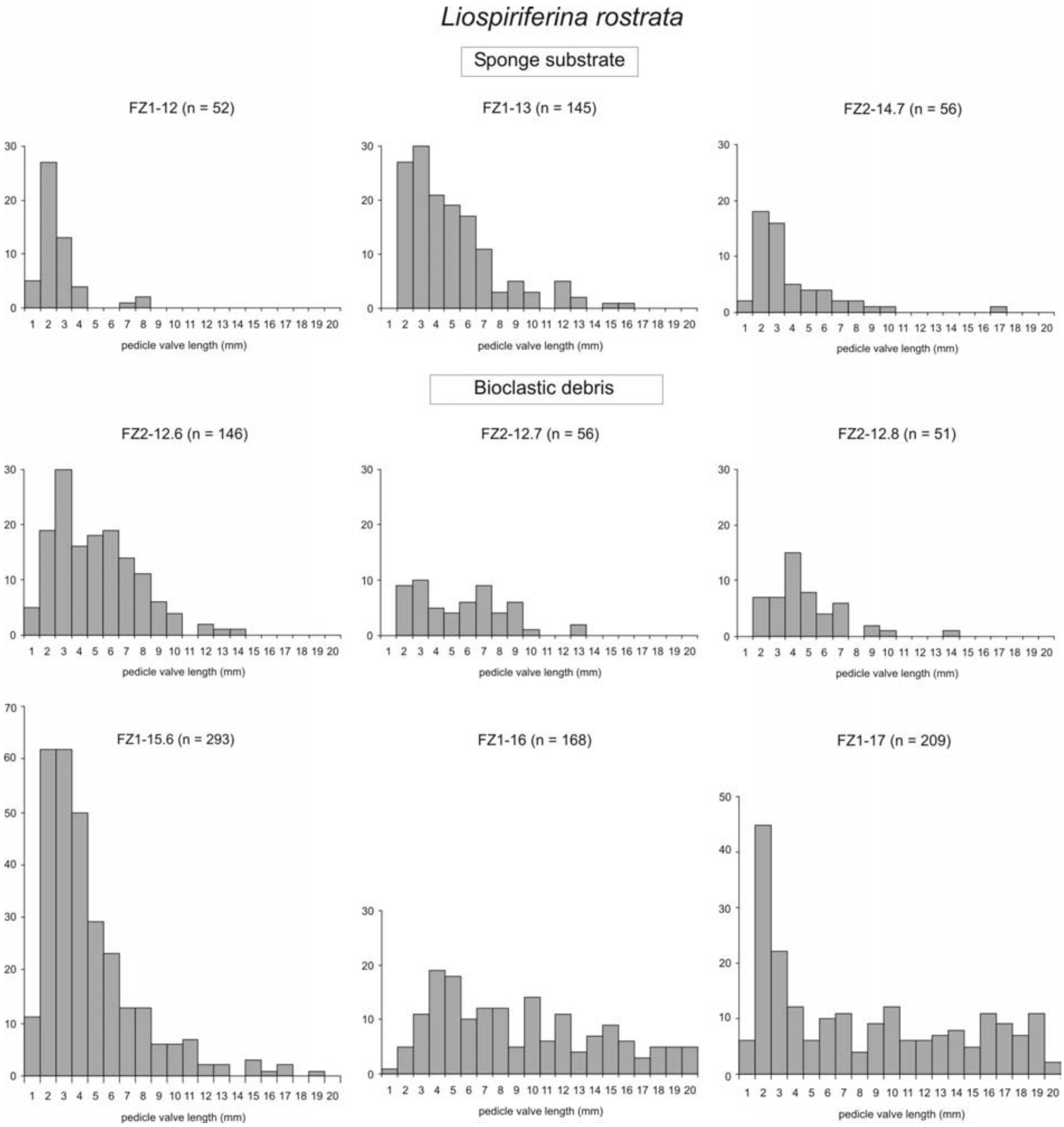


Figure 19 – Differences in size-frequency distributions of *Liospiriferina rostrata* between sponge and bioclast-rich substrates. For comparison with assemblages from microbial crusts, see Figure 18.

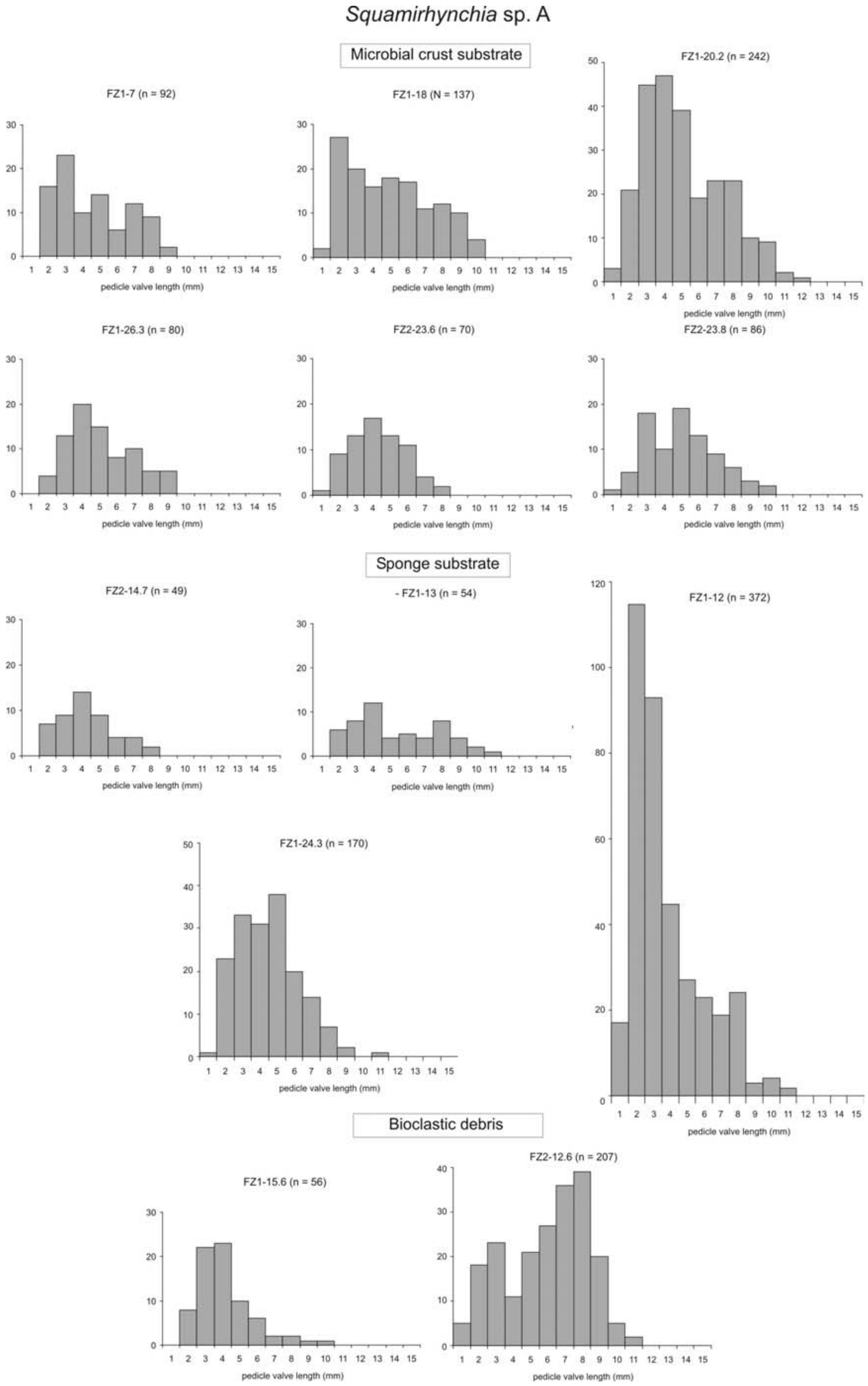


Figure 20 – Between-substrate differences in size-frequency distributions of *Squamirhynchia* sp. A.

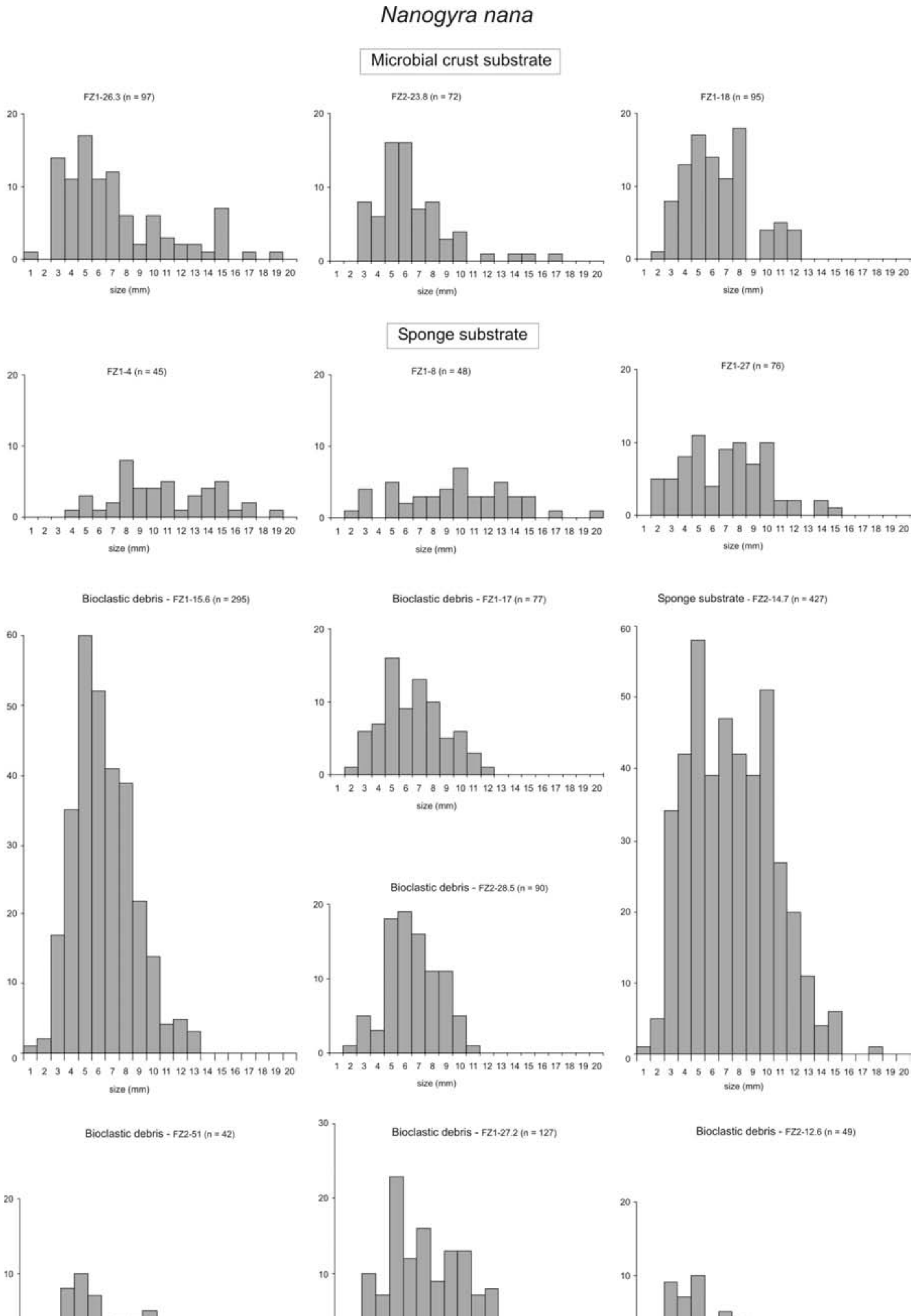


Figure 21 – Between-substrate differences in size-frequency distributions of *Nanogyra nana*.

Zeilleria rehmanni	Shelliness	Median (mm)	n	Skewness	Kurtosis	Median (> 5 mm)	n (median > 5 mm)	Ix (5 mm)
FZ1-35 - brachiopod shell bed	dense	17	50	-1.102	1.535	17	50	100
FZ1-36-1 - brachiopod shell bed	dense	17	37	-0.892	-0.496	17.3	34	91.9
FZ1-36-2 - brachiopod shell bed	dense	16.5	29	-0.25	-1.026	16.5	29	100
FZ2-23.6 - microbial crusts	dispersed	4.3	159	2.798	8.8	6.8	57	56
FZ2-23.8 - microbial crusts	dispersed	4.3	94	1.727	2.033	9.5	36	53.2
FZ1-40 - microbial crusts	dispersed	7.3	33	0.41	-1.14	8.6	33	84.8
FZ5-40 - microbial crusts	dispersed	11.2	45	0.423	-0.83	11.9	44	97.8
FZ1-26.3 - microbial crusts	loose	5.1	74	0.947	-0.679	12.5	39	70.3
FZ1-38.2 - microbial crusts	loose	8.8	65	0.244	-1.387	10.2	54	90.7
FZ2-25 - microbial crusts	loose	6	70	1.348	0.663	8.6	45	72.9
FZ2-51 - bioclastic debris	loose	6.3	31	0.667	-0.856	11	18	77.4
Zeilleria vicinalis	Shelliness	Median (mm)	n	Skewness	Kurtosis	Median (> 5 mm)	n (median > 5 mm)	Ix (5 mm)
FZ1-4 - sponge	shell-poor	4.3	40	2.273	5.201	6.7	16	60
FZ1-12 - sponge	shell-poor	4.1	67	1.201	1.189	8.1	20	52.2
FZ1-13 - sponge	shell-poor	4.3	80	2.151	4.99	8.8	37	52.5
FZ2-14.7 - sponge	shell-poor	4.5	45	1.566	2.436	7.3	17	57.8
FZ2-13 - microbial crusts	shell-poor	5.4	41	1.444	1.152	7.8	21	61
FZ2-7.3 - microbial crusts	shell-poor	4.5	43	1.829	3.839	7.1	16	55.8
FZ1-7 - microbial crusts	shell-poor	4	71	1.197	0.162	10.5	26	47.9
FZ1-5 - microbial crusts	shell-rich	8.7	132	-0.235	-1.013	9.6	105	78
FZ2-12.6 - bioclastic debris	shell-rich	8	209	0.136	-1.162	11.5	154	78.9
FZ2-12.7 - bioclastic debris	shell-rich	7.7	94	0.285	-1.378	13.5	60	74.5
FZ2-12.8 - bioclastic debris	shell-rich	5.8	66	0.958	-0.154	10.9	36	60.6
Liospiriferina rostrata	Shelliness	Median (mm)	n	Skewness	Kurtosis	Median (> 5 mm)	n (median > 5 mm)	Ix (5 mm)
FZ1-12 - sponge	dispersed	1.7	52	2.307	5.6	7.2	3	5.8
FZ1-13 - sponge	dispersed	3.6	145	1.487	2.192	6.5	48	46.2
FZ2-14.7 - sponge	dispersed	2.2	56	2.409	7.716	6.8	11	26.8
FZ1-15.6 - bioclastic debris	dispersed	3.3	293	1.775	3.585	7.3	79	36.9
FZ2-23.6 - microbial crusts	dispersed	3.1	63	1.21	1.151	6.9	9	25.4
FZ1-7 - microbial crusts	dispersed	2.7	102	1.337	0.561	9	27	29.4
FZ2-12.6 - bioclastic debris	loose	4.3	146	0.802	0.384	6.7	58	52.1
FZ2-12.7 - bioclastic debris	loose	5.1	56	0.479	-0.389	6.9	28	57.1
FZ2-12.8 - bioclastic debris	loose	3.6	51	1.457	3.231	6.5	14	43.1
FZ1-5 - microbial crusts	loose	4.3	66	0.428	-0.944	7.6	27	56.1
FZ1-26.3 - microbial crusts	loose	3.3	49	1.174	0.901	7.2	15	40.8
FZ1-5-40 - microbial crusts	loose	5.3	51	0.679	-0.237	7.1	28	72.5
FZ2-7.3 - microbial crusts	loose	3.1	61	0.914	-0.747	10.5	19	41
FZ2-13 - microbial crusts	loose	4.2	49	1.177	0.549	6.4	29	50.7
FZ2-25 - microbial crusts	loose	2.7	57	2.685	8.8	8.1	10	22.8
FZ1-16 - bioclastic debris	dense	7.6	168	0.484	-0.89	10.9	114	78.6
FZ1-17 - bioclastic debris	dense	6.7	209	0.454	-1.215	12.2	121	59.3
Squamirhynchia sp. A	Shelliness	Median (mm)	n	Skewness	Kurtosis	Median (> 5 mm)	n (median > 5 mm)	Ix (5 mm)
FZ1-7 - microbial crusts	dispersed	3.5	92	0.472	-1.077	6.8	29	46.7
FZ1-18 - microbial crusts	dispersed	4.1	137	0.33	-1.067	6.8	54	52.6
FZ1-20.2 - microbial crusts	dispersed	4.1	242	0.593	-0.402	7.1	85	52.1
FZ1-26.3 - microbial crusts	dispersed	4.2	80	0.496	-0.811	6.8	28	53.8
FZ2-23.6 - microbial crusts	dispersed	3.8	70	0.2	-0.785	5.5	17	42.9
FZ2-23.8 - microbial crusts	dispersed	4.6	86	0.322	-0.592	6.6	33	60.5
FZ2-14.7 - sponge	dispersed	3.8	49	0.582	-0.565	6.5	10	38.8
FZ1-13 - sponge	dispersed	4.2	54	0.35	-1.0944	7.5	24	51.9
FZ1-12 - sponge	dispersed	2.5	372	1.132	0.436	6.7	75	27.4
FZ1-24.3 - sponge	dispersed	3.9	170	0.566	0.034	6.2	44	48.2
FZ1-15.6 - bioclastic debris	dispersed	3.3	56	1.284	1.585	6.2	12	29.3
FZ2-12.6 - bioclastic debris	dispersed	5.9	207	-0.328	-0.949	7	129	72.5

Table 6 - Summary of size-frequency distributions in terms of their standard parametric descriptors.

Nanogyra nana	Shelliness	Median (mm)	n	Skewness	Kurtosis	Median (> 5 mm)	n (median > 5 mm)	Ix (5 mm)
FZ1-4 - sponge	shell-poor	9.9	45	0.175	0.881	10.3	41	97.8
FZ1-8 - sponge	shell-poor	9.1	48	0.177	-0.425	10.1	38	89.6
FZ1-27 - sponge	shell-poor	5.4	76	1.064	0.35	7.9	55	73.2
FZ2-14.7 - sponge	shell-poor	5.6	427	1.55	3.284	6.6	42	80.6
FZ1-26.3 - microbial crusts	shell-poor	5.8	97	0.553	-0.278	7.1	56	76.8
FZ2-23.8 - microbial crusts	shell-poor	5.8	72	0.332	-0.581	7.2	47	81.8
FZ1-18 - microbial crusts	shell-poor	4.33	95	1.356	2.542	7.5	20	59.2
FZ1-15.6 - bioclastic debris	shell-poor	5.2	295	0.505	-0.9	7.4	22	76.2
FZ1-17 - bioclastic debris	shell-rich	6.6	77	0.251	-0.577	8.3	47	76.3
FZ2-12.6 - bioclastic debris	shell-rich	6.8	49	0.388	-0.44	8.3	289	80.8
FZ2-28.5 - bioclastic debris	shell-rich	5.8	90	0.551	0.237	6.8	181	81.4
FZ2-51 - bioclastic debris	shell-rich	5.9	42	0.066	-0.5	6.6	63	90
FZ1-27.2 - bioclastic debris	shell-rich	6.6	127	0.344	-0.595	8.3	84	84.3

Table 6 (continued) - Summary of size-frequency distributions in terms of their standard parametric descriptors.

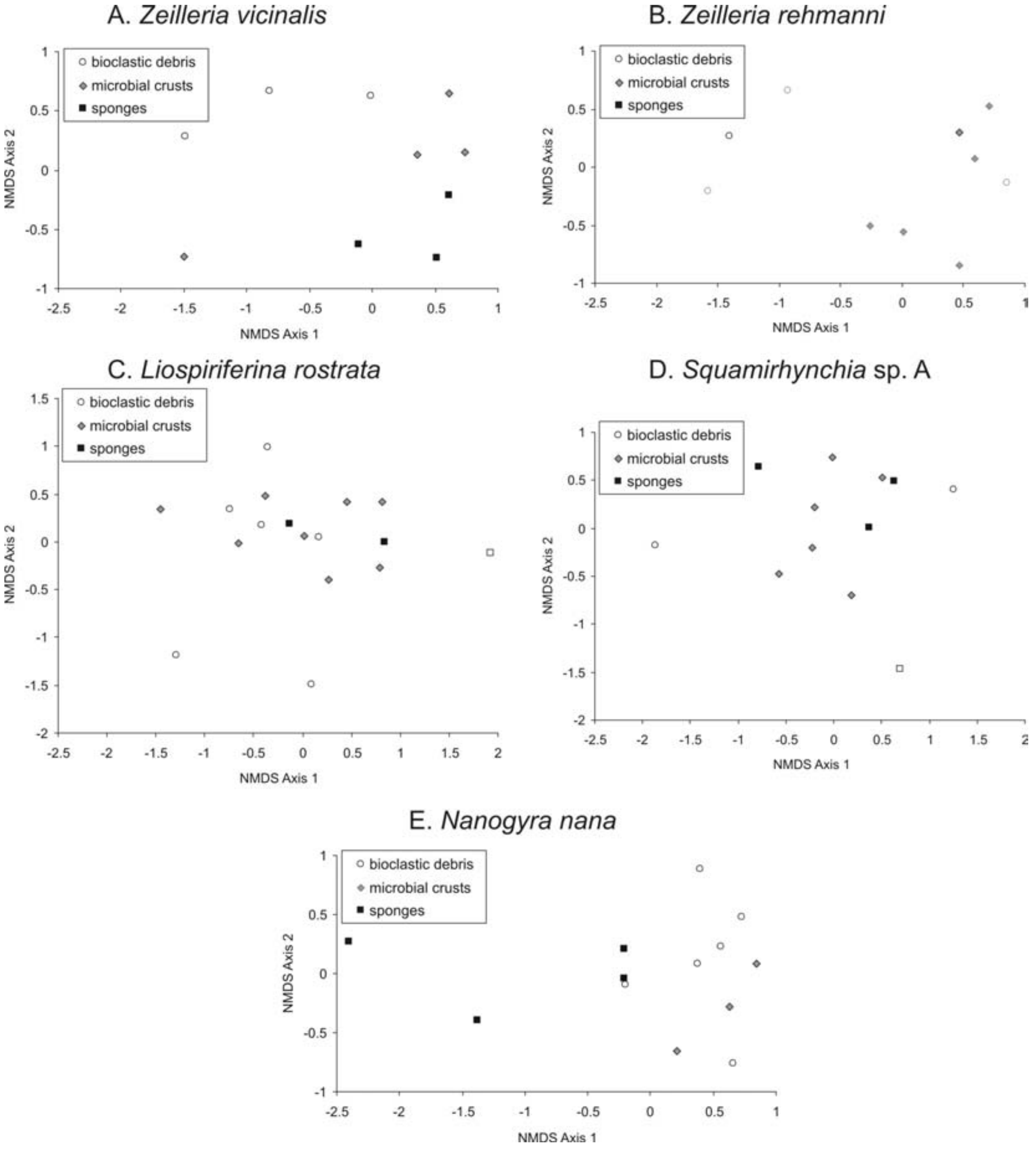


Figure 22 – NMDS of size-frequency distributions showing between-substrate differences in four brachiopods and one bivalve species. A. *Zeilleria vicinalis*. B. *Zeilleria rehmanni*. C. *Liospiriferina rostrata*. D. *Squamirhynchia* sp. A. E. *Nanogyra nana*.

Between-habitat within-species comparisons. One-way ANOSIM consistently indicates that between-habitat differences in SFDs are very low and insignificant for five species (Tab. 7). There are also no consistent differences in median size, skewness or kurtosis among habitats. No effects of wave-base level on SFDs also follow from two-way analyses of *Zeilleria rehmanni* and *Liospiriferina rostrata*. Allowing for substrate variations, between-habitat differences in SFDs of *Nanogyra nana* are of borderline significance (two-way ANOSIM, R = 0.52, p = 0.05).

Size-specific survivorship and mortality curves. Between-habitat differences in survivorship are very low. Therefore, comparative analysis is focused on between-substrate differences in survivorship. *Zeilleria vicinalis* on sponge substrates has concave survivorship curves and high juvenile mortality rates. In contrast, *Z. vicinalis* from substrates formed by bioclasts shows convex survivorship curves and low juvenile mortality rates (Figs. 23A, 24A). Survivorship and mortality rates of *Z. vicinalis* assemblages from microbial crusts are variable. *Zeilleria rehmanni* from substrates formed by bioclasts is characterized by more convex survivorship curves than *Zeilleria rehmanni* from substrates formed by microbial crusts. Juvenile mortality rates of *Zeilleria rehmanni* from the brachiopod shell bed are minimal, in contrast to those from microbial crusts (Figs. 23B, 24B). *Liospiriferina* is characterized by a high variation in shape of survivorship curves. The assemblages from sponge substrates are represented by concave survivorship curves and bioclast-rich substrates by convex curves (Fig. 23C). The curves from microbial crusts are intermediate in shape, although some are characterized by highly concave shape. The assemblages from sponge substrates show the highest juvenile mortality rates (Fig. 24C). *Squamirhynchia* shows poor between-substrate differences in survivorship curves and juvenile mortality rates (Figs. 23D, 24D). *Nanogyra nana* from sponge substrates is characterized by survivorship curves with higher convexity and lower juvenile mortality *Nanogyra nana* from substrates formed by microbial crusts and bioclasts (Figs. 23E, 24E).

Between-habitat/substrate differences in size-frequency distributions	R Statistic	p-value	Permutations	Number of permuted R≥observed R
Zeilleria vicinalis				
One-way-habitat	-0.04	0.53	462	247
One-way-substrate	0.34	0.033	5775	188
Zeilleria rehmanni				
One-way-habitat	0.156	0.13	330	43
One-way-substrate	0.519	0.021	330	7
Two-way - habitat (constant substrate)	0.423	0.079	140	11
Two-way - substrate (constant habitat)	0.887	0.07	140	1
Liospiriferina rostrata				
One-way-habitat	0.065	0.25	10000	2506
One-way-substrate	0.086	0.2	10000	1996
Two-way - habitat (constant substrate)	-0.26	0.91	840	757
Two-way - substrate (constant habitat)	0.086	0.32	1680	534
Squamirhynchia sp. A				
One-way-habitat	-0.005	0.47	5544	2586
One-way-substrate	0.229	0.081	10000	811
Nanogyra nana				
One-way-habitat	-0.067	0.68	1287	870
One-way-substrate	0.267	0.034	10000	336
Two-way - habitat (constant substrate)	0.518	0.05	60	3
Two-way - substrate (constant habitat)	0.463	0.008	1400	11

Table 7 – Analyses of similarities (ANOSIM) testing between-habitat and between-substrate differences in size-frequency distributions. One-way analyses were performed for each species. If the two-way crossed sampling design was possible, two-way analyses were also performed.

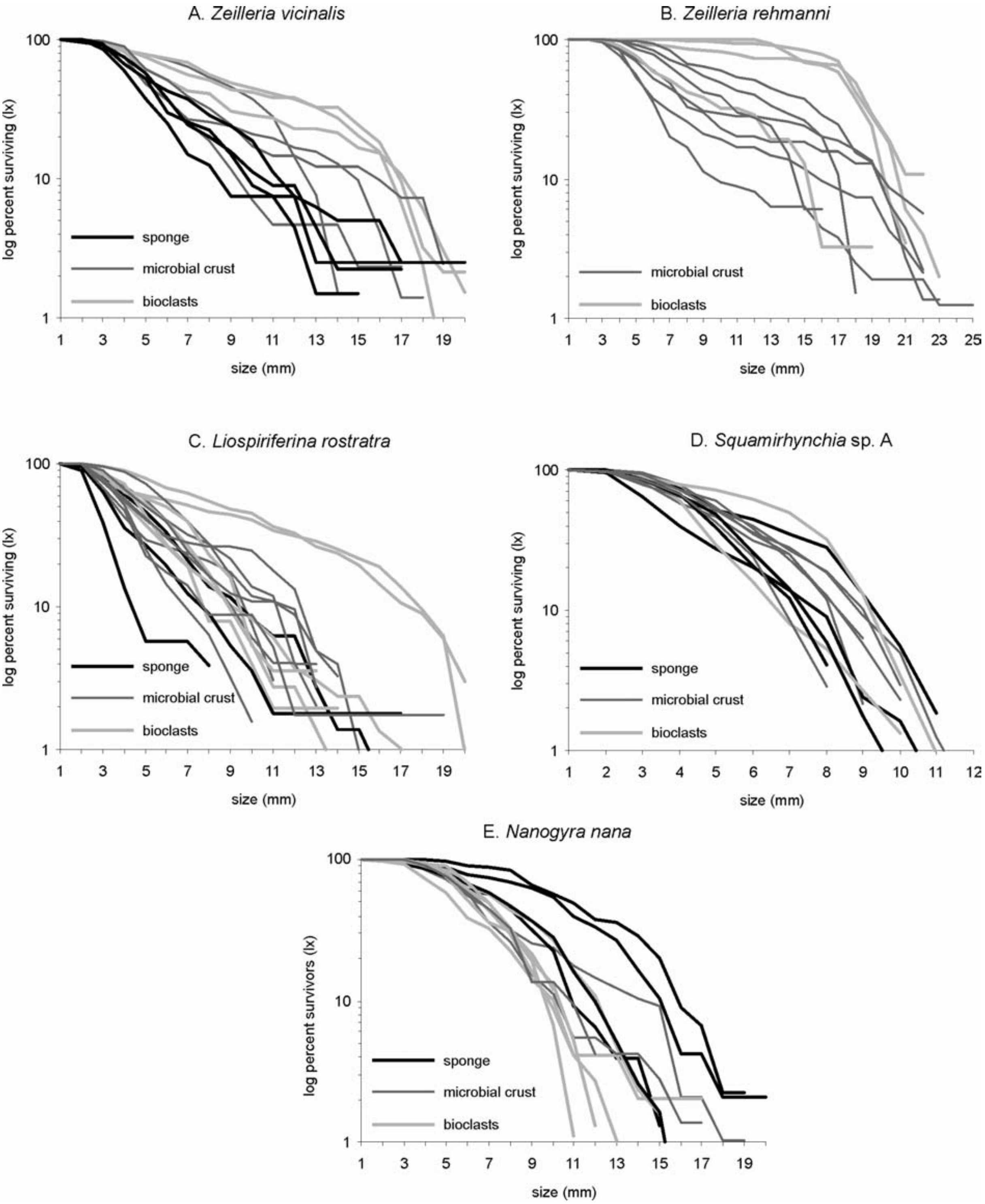


Figure 23 – Between-substrate differences in survivorship curves of four brachiopod species and *Nanogyra nana*. *Zeilleria vicinalis* and *Liospiriferina rostrata* show lower juvenile mortality on bioclastic than on sponge substrates. *Nanogyra* shows higher juvenile mortality on bioclastic than on sponge substrates. *Zeilleria rehmanni* shows higher juvenile mortality on microbial crusts than on bioclastic substrates. The rhynchonellid *Squamirhynchia* sp. A does not show any between-substrate differences in survivorship curves.

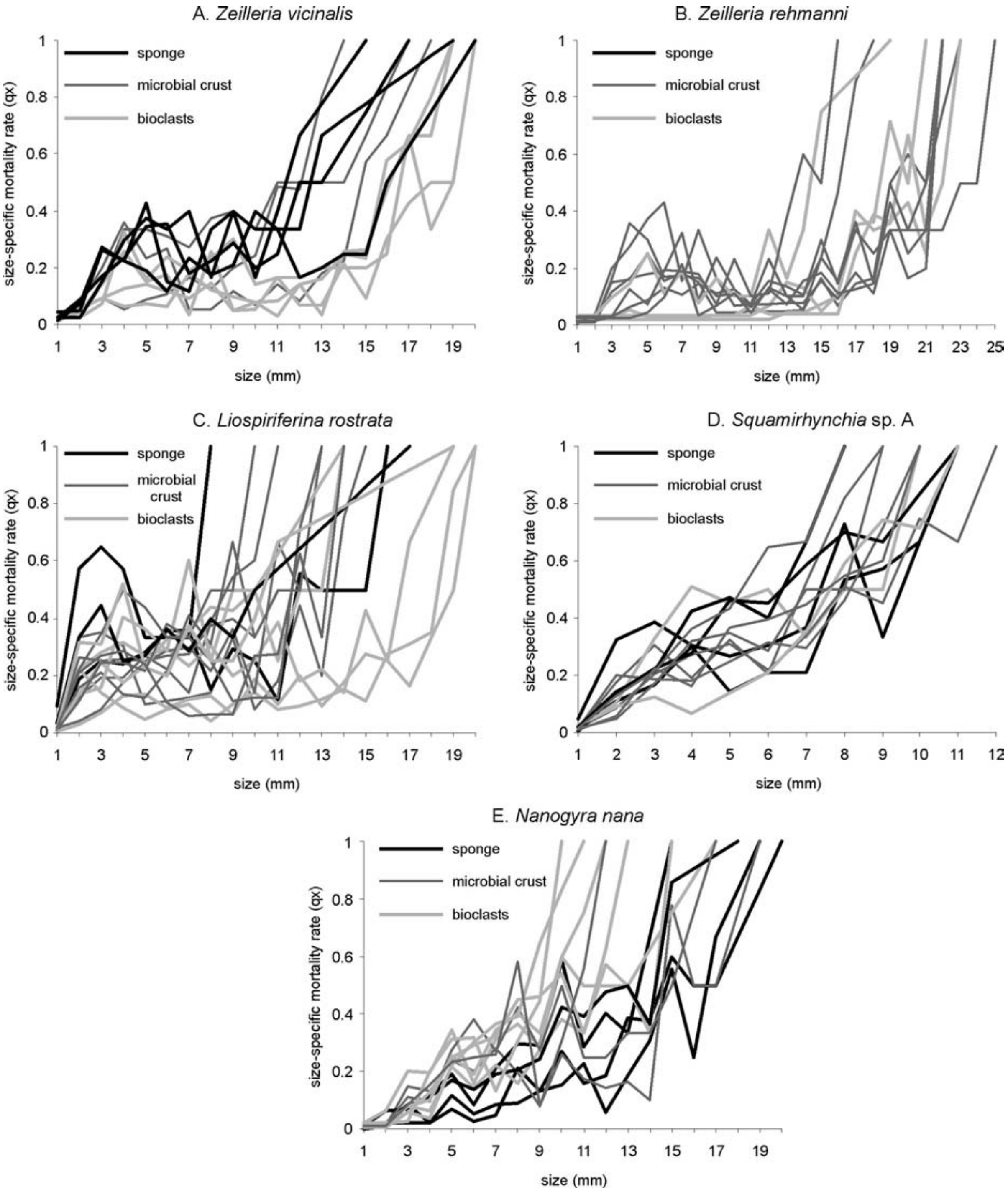


Figure 24 - Between-substrate differences in size-specific mortality rates of four brachiopod species and *Nanogyra nana*. Juvenile mortality of *Zeilleria vicinalis* and *Liospiriferina rostrata* is higher on sponge substrates and lower on bioclastic substrates. *Nanogyra nana* shows the opposite pattern.

Linking juvenile mortality rates to community-level abundances

Finite mortality rates of juveniles < 5 mm and community-level relative abundances of individuals > 5 mm were compared on genus level among *Nanogyra, Zeilleria, Squamirhynchia* and *Liospiriferina*. In addition, juvenile mortality rates of three brachiopod genera were compared with abundances of adult cementing bivalves, and juvenile mortality rates of *Nanogyra* were compared with abundances of adult pedunculate brachiopods. Therefore, five pairwise comparisons were performed for each genus (Tab. 8). Negative Spearman rank correlation between juvenile mortality rates and adult community-level abundances is high and significant for *Nanogyra* (r = -0.73, p = 0.005)*,* *Zeilleria* (r = -0.84, p < 0.0001) and *Liospiriferina* (r = -0.596, p = 0.0116) and insignificant for *Squamirhynchia* (r = 0.2, p = 0.5). There is a positive correlation between juvenile mortality rates of *Nanogyra* and abundance of adult pedunculate brachiopods (r = 0.75, p = 0.0033), *Squamirhynchia* r = 0.8, p = 0.0009), and *Liospiriferina* (r = 0.58, p = 0.036, Fig. 25). The correlation between juvenile mortality rates of *Nanogyra* and abundance of adult *Zeilleria* is insignificant (r = 0.35, p = 0.23). If one outlier (Sample FZ1-4) is removed, the correlation is higher (r = 0.59) and of borderline significance (p = 0.049). There is also a positive Spearman rank correlation between juvenile mortality rates of *Zeilleria* and abundance of adult cementing bivalves (r = 0.57, p = 0.0072) and *Nanogyra* (r = 0.59, p = 0.0053, Fig. 26). Juvenile mortality rate of *Zeilleria* does not correlate with adult abundances of *Liospiriferina* and *Squamirhynchia* (Tab. 8). Spearman rank correlations between juvenile mortality rates of *Liospiriferina* and *Squamirhynchia* and adult abundances of other genera are invariably low and insignificant (Tab. 8).

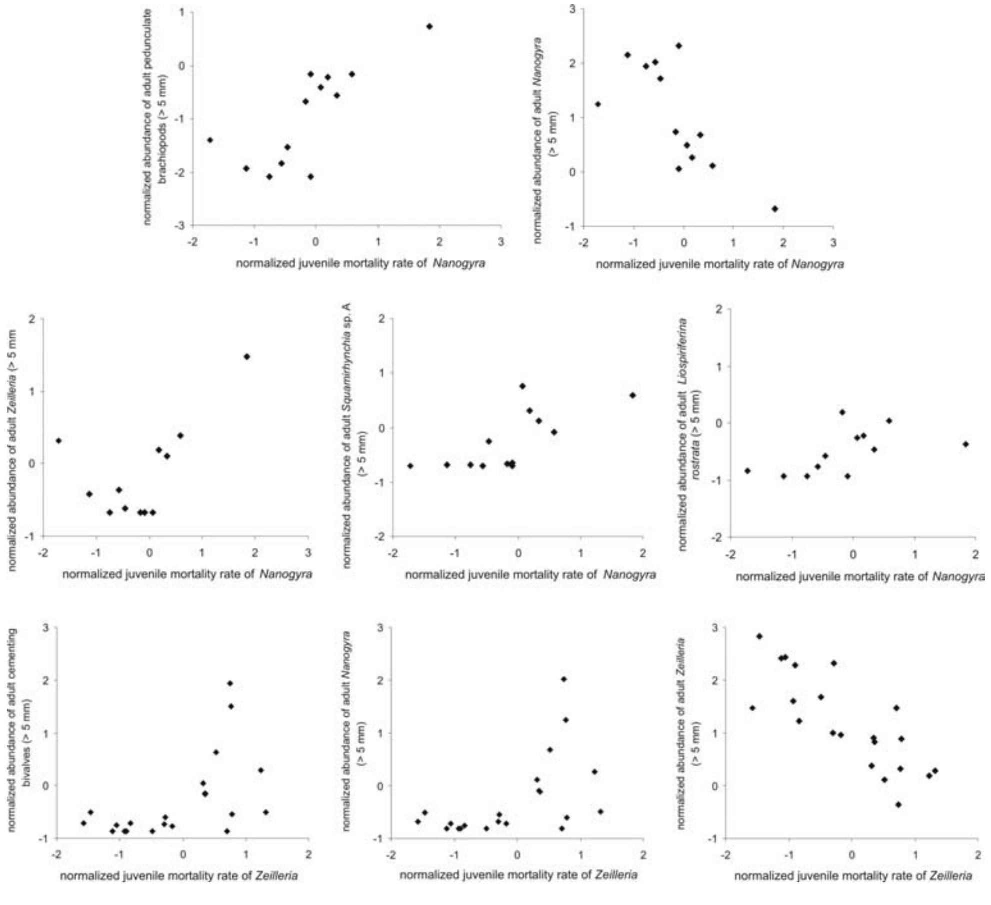


Figure 25 – Correlations between juvenile mortality rates and community-level abundance of adults.

Relationship between juvenile mortality rates and community-level abundances	Spearman rs	p-value
Juvenile mortality rate of *Nanogyra* vs. abundance of adult pedunculate brachiopods	**0.748**	**0.0033**
Juvenile mortality rate of *Nanogyra* vs. abundance of adult *Nanogyra*	**-0.724**	**0.0052**
Juvenile mortality rate of *Nanogyra* vs. abundance of adult *Zeilleria*	0.353	0.237
Juvenile mortality rate of *Nanogyra* vs. abundance of adult *Squamirhynchia* sp. A	**0.803**	**0.0009**
Juvenile mortality rate of *Nanogyra* vs. abundance of adult *Liospiriferina rostrata*	**0.584**	**0.036**
Juvenile mortality rate of *Zeilleria* vs. abundance of adult cementing bivalves	**0.569**	**0.0072**
Juvenile mortality rate of *Zeilleria* vs. abundance of adult *Zeilleria*	**-0.834**	**<0.0001**
Juvenile mortality rate of *Zeilleria* vs. abundance of adult *Liospiriferina rostrata*	0.152	0.51
Juvenile mortality rate of *Zeilleria* vs. abundance of adult *Squamirhynchia* sp. A	0.193	0.403
Juvenile mortality rate of *Zeilleria* vs. abundance of adult *Nanogyra*	**0.586**	**0.0053**
Juvenile mortality rate of *Squamirhynchia* sp. A vs. abundance of adult cementing bivalves	0.07	0.823
Juvenile mortality rate of *Squamirhynchia* sp. A vs. abundance of adult *Squamirhynchia* sp. A	0.201	0.513
Juvenile mortality rate of *Squamirhynchia* sp. A vs. abundance of adult *Liospiriferina rostrata*	0.063	0.846
Juvenile mortality rate of *Squamirhynchia* sp. A vs. abundance of adult *Zeilleria*	-0.225	0.481
Juvenile mortality rate of *Squamirhynchia* sp. A vs. abundance of adult *Nanogyra*	0.074	0.82
Juvenile mortality rate of *Liospiriferina rostrata* vs. abundance of adult cementing bivalves	0.152	0.56
Juvenile mortality rate of *Liospiriferina rostrata* vs. abundance of adult *Liospiriferina* sp.	**-0.596**	**0.0116**
Juvenile mortality rate of *Liospiriferina rostrata* vs. abundance of adult *Squamirhynchia* sp. A	0.333	0.19
Juvenile mortality rate of *Liospiriferina rostrata* vs. abundance of adult *Zeilleria*	-0.104	0.69
Juvenile mortality rate of *Liospiriferina rostrata* vs. abundance of adult *Nanogyra*	0.17	0.51

Table 8 – Spearman rank correlation coefficients between juvenile mortality rates and relative abundances of adults. Normalized mortality rates of juvenile brachiopods and bivalves are defined for specimens that attain less than 5% of their maximum adult size. Normalized relative abundance of adults is defined for specimens larger than 5 mm.

Relationship between shell density and population dynamics

To evaluate whether there is any relationship between population dynamics and shell density, differences between shell-rich and shell-poor samples in juvenile survivorship and adult median size (> 5 mm) were evaluated for *Zeilleria vicinalis, Z. rehmanni*, *Liospiriferina rostrata* and *Nanogyra nana* (Fig. 26). *Zeilleria vicinalis* shows significantly higher survivorship of juveniles in shell-rich samples (median = 76%) than in shell-poor samples (median = 55.8%). It also shows a significantly higher adult median size in shell-rich (11.2 mm) than in shell-poor samples (7.8 mm). Similarly, *Zeilleria rehmanni* shows significantly higher survivorship of juveniles in shell-rich samples (median = 100%) than in shell-poor samples (median = 75%), and a significantly higher adult median size in shell-rich (17 mm) than in shell-poor samples (9.9 mm). *Liospiriferina rostrata* shows significantly higher survivorship of juveniles in shell-rich samples (median = 52%) than in shell-poor samples (median = 28%). However, differences in adult median size between shell-rich (7.2 mm) and in shell-poor samples (7.1 mm) are insignificant. *Nanogyra nana* does not show any significant differences in juvenile survivorship between shell-rich (median = 81.4%) and shell-poor samples (median = 78.7%). Similarly, differences in adult median size between shell-rich (8.3 mm) and shell-poor samples (7.5 mm) are very small.

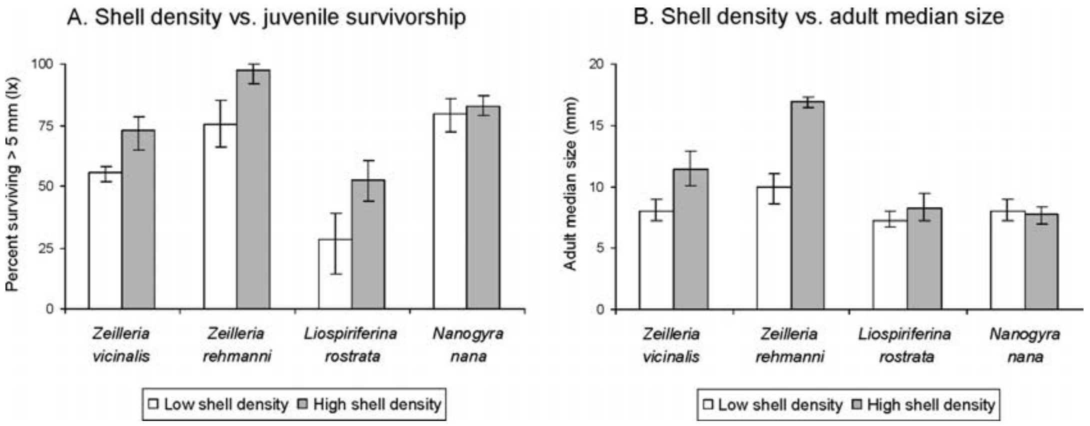


Figure 26 – Relationship between shell density and population dynamics. A. Differences in juvenile survivorship between shell-poor and shell-rich samples. B. Differences in adult median size between shell-poor and shell-rich samples.

Discussion

Effects of flow speed on abundance and survivorship. Although there were no consistent differences among communities dominated by brachiopods and epifaunal bivalves, or in abundance patterns among brachiopods and epifaunal bivalves, the most abundant guilds represented by pedunculate brachiopods and cementing oysters show substantial differences in abundance patterns and environmental distribution. These differences imply that both groups differed in their response to an environmental gradient. Minimum amount of siliciclastic admixture, absence of signs of long-term high-energy conditions, and abundance of hard substrates indicate that although habitats differed in storm frequency and intensity, they do not reflect highly variable and complex environmental gradients. The differences among habitats between normal and maximum storm wave base probably reflect small-scale variations in episodic storm events and background flow speeds, although environmental factors such as light intensity and oxygen levels might have co-varied with the wave-base level gradient.

Between-habitat differences in the abundance of brachiopods and oysters are partly in accord with actualistic expectations about their habitat preferences. Brachiopods may prefer deeper habitats with lower flow speeds than cementing bivalves because of differences in their feeding mechanisms. Brachiopods have lower pumping and clearance rates than bivalves under comparable particle concentrations (Rhodes and Thompson, 1992, 1993). First, differences in flow speeds substantially influence particle flux and thus also food availability (Butman et al., 1994; Leichter and Witman, 1997). Food can be rapidly depleted under reduced flow speeds in the motionless benthic boundary layer. Food depletion is less likely under turbulent mixing. Both brachiopods and epifaunal bivalves with filibranch and pseudolamellibranch gills can cope with depleted food supply. Brachiopods have low metabolic requirements and are efficient in water transport through the mantle cavity (LaBarbera, 1981b, 1984). Epifaunal bivalves have higher metabolic demands but also higher clearance rates than rhynchonelliformean brachiopods (LaBarbera, 1981b; Rhodes and Thompson, 1992, 1993). Second, the flow speed affects the energetics of suspension-feeding (Eckman and Duggins, 1993; Lenihan et al., 1996; Genovese and Witman, 1999; Okamura et al., 2001). Bivalve feeding rates respond non-monotonically to varying flow speeds because moderate flow speeds promote feeding rates of bivalves but very low or very high levels inhibit them (Ackerman and Nishizaki, 2004). On one hand, feeding rates decline under reduced flow speeds. It is expected that preferred ambient flow speeds for suspension-feeding bivalves will approximate the inhalant pumping speeds (Grizzle et al., 1992). On the other hand, high flow velocities affect the pressure differential between the inhalant and exhalant currents against which suspension-feeders must pump (Wildish et al., 1987, Wildish and Miyares, 1990). In addition, very high flow speeds cause drag effects, and may deform filtering structures and reduce surface areas for particle capture (Okamura and Partridge, 1999). Therefore, reduced flow speeds are suboptimal for bivalves that have higher pumping speeds than brachiopods. In contrast, the ability of brachiopods to feed under high flow speeds might be limited and they can be more efficient at lower flow speeds. Differential abundance of bivalves and brachiopods may thus reflect their different abilities to feed efficiently under varying flow speeds. Gahr (2005) assumed that the differential distribution of brachiopods and bivalves with respect to particle flux is related to the ability of brachiopods to directly absorb dissolved organic matter (McCammon, 1969; McCammon and Reynolds, 1976; Steele-Petrović, 1976; Doherty, 1981). However, bivalves are also able to use dissolved organic matter (Wright, 1982; Rice and Stephens, 1987; Dame, 1996; Chiantore et al., 1998) so this aspect of feeding strategy cannot account for lower abundance of epifaunal bivalves in food-limited, low-energy habitats. In addition, the contribution of direct absorption to the energetic requirements of brachiopods is probably small (Tkachuck et al., 1989).

Size-frequency distributions do not show any clear evidence for substantial effects of habitat on survivorship. However, the presented results can be affected by two factors. First, habitat effects can be confounded by substrate effects. Two-way analysis of SFDs of *Nanogyra nana* allowing for substrate variations indicates significant habitat effects. However, habitat effects are insignificant for *Zeilleria rehmanni* and *Liospiriferina rostrata* even when the substrate type is kept constant. Sampling design does not allow evaluating this effect for *Zeilleria vicinalis*. Second, SFDs were restricted only to samples with high specimen numbers, thus preferentially analysing sites with higher species abundance. For example, SFDs of *Nanogyra* were not available from deep habitats. Between-habitat differences in SFDs might be higher if samples with low community-level abundance are also analysed.

High juvenile mortality of brachiopods - effect of competition for space. All three substrate types are interpreted here as representing mixed- and hard-bottom conditions with long-lived hard substrates (sponges, microbial crusts), live brachiopod and bivalve shells, ephemeral shell debris and presence of carbonate mud. Between-substrate differences are interpreted here mainly in terms of differences between sponges and microbial crusts. Although abundance and survivorship patterns of epifaunal bivalves and brachiopods on substrates formed by bioclasts, commonly formed by shells of conspecifics, can be related to positive effects of substrate on their growth and survival, they may also represent a passive response to high abundance of shell-producers (i.e., a peak in abundance of brachiopods inevitably produces brachiopod-rich substrate). Abundance peaks of brachiopods and bivalves simply correspond to brachiopod or bivalve shell beds. Although between-substrate differences in recruitment are not constrained, survivorship patterns demonstrate that variations in abundances were driven by variations in mortality rates. The correspondence between community-level abundance and survivorship patterns also indicates that relative abundance patterns reflect real differences in absolute abundances, rather than being a passive response to changes in absolute abundances of some groups only (Finnegan and Droser, 2005). Two lines of evidence indicate that between-substrate differences in abundance and survivorship patterns are related to combined effects of varying flow speeds and varying competition intensity.

First, abundances of sponges and microbial crusts were partly related to long-term variations in wave-base level. Microbial crusts were produced and preserved mainly in deep habitats below NSWB and MSWB. Their thickness decreased towards shallow environments. The abundance of microbial crusts was highest in units with lowest frequency of storm-reworked beds – mainly in lowermost (unit 1) and uppermost (unit 6) parts of the lower member of the Foum Zidet Formation. Environmental conditions in deep habitats were locally favorable for growth of microbial crusts. These conditions were thus partly depth-dependent and might also be driven by differences in flow speeds. A long-term decrease in storm activity might be related to reduced water mixing and circulation, possibly also leading to reduced oxygen concentrations in deep habitats. Reduced oxygen levels are supposed to be one of the substantial agents promoting formation and preservation of microbial crusts (Leinfelder et al., 1993; Dupraz and Strasser, 1999). Microbial crusts were rare and sponges dominated during some time intervals in deep habitats (e.g., in units 3-4), implying that reduced water mixing and environmental restriction did not completely correlate with water depth or wave-base level. However,the differential effect of varying flow speeds on suspension-feeding of brachiopods and bivalves may also be responsible for abundance and survivorship differences among substrates. Higher abundances of oysters on sponge substrates and higher abundances of brachiopods on microbial crusts thus imply that oysters shared habitat preferences with sponges, and brachiopods with microbial crusts. For example, distribution of present-day sponges is related to flow speeds because they are limited in habitats with very low flow speeds (Rice et al., 1990; Starmans et al., 1999; Klitgaard and Tendal, 2004).

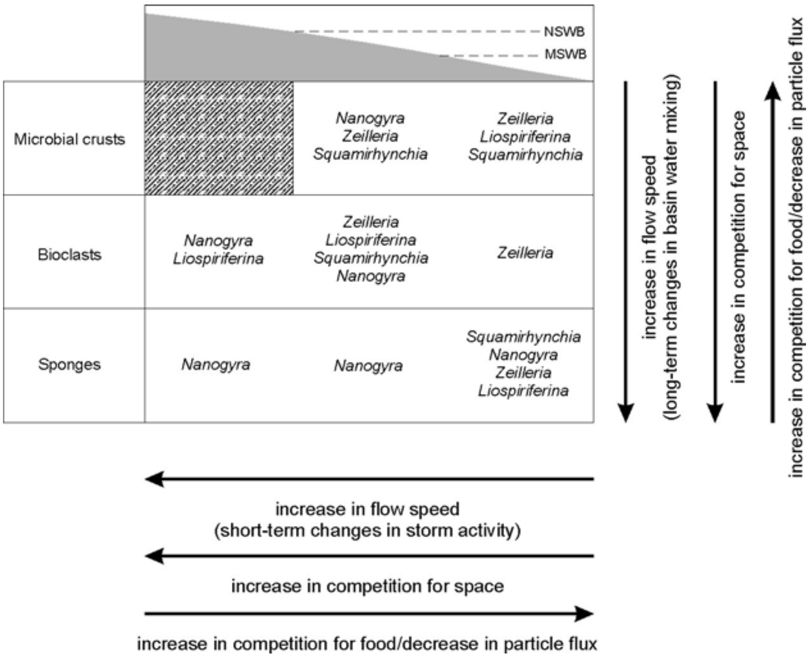


Figure 27 – Variations in dominance of brachiopod and bivalve genera of the Foum Zidet Formation along gradients with varying wave-base level and substrate composition. Genera attaining more than 10% in community-level abundance are shown (based on specimens > 5 mm).

Second, based on volumetric abundances of biotic components in thin-sections, sponges were significantly more frequently covered by shelly encrusters than microbial crusts. The difference in percent cover of encrusters implies that microbial crusts dominated in habitats with reduced intensity of competition for space, in contrast to sponges. The first alternative explanation would be that microbial crusts limited settlement of encrusters and epibionts owing to some physical or chemical properties. For example, their soft consistency might inhibit larvae requiring hard substrate if the calcification rate of microbial crusts was too slow. This alternative can be excluded because larvae of encrusters such as bryozoans, *Terebella*, *Radiomura* and *Tubiphytes* that are more common on microbial crusts than on sponge substrates probably required similar substrate consistency as larvae of oysters or serpulids. In addition, deposits dominated by microbial crusts invariably contain also shells and sponges that can provide settlement with sufficient consistency. However, brachiopod shells or sponge fragments in such deposits are also affected by low proportion of encrusters.

High community-level abundance and low mortality of cementing bivalves on sponges imply their greater ability to compete for space. In general, present-day bivalves are characterized by higher growth rates than brachiopods (Rosenberg et al., 1988). With this reasoning, slow-growing and especially juvenile, small-sized brachiopods with restricted mobility were affected by high mortality on sponge substrates owing to high probability of overgrowth. The two explanations related to distinct habitat preferences and distinct competition abilities of brachiopods and bivalves are not mutually exclusive. It is probable that higher community-level abundance of brachiopods on microbial crusts in deep habitats reflects combined effects of reduced flow speed that limited performance of bivalves and sponges, and reduced intensity of competition for space (Fig. 28). Note that between-substrate differences in juvenile survivorship imply that the distribution pattern of brachiopods and cementing bivalves was rooted in differential ecology of their *juveniles*. This is also supported by the significant correlations between their juvenile mortality rates and community-level abundances that indicate out-of-phase environmental preferences of *juvenile* brachiopods and bivalves, and/or negative competitive juvenile-adult interactions between brachiopods and oysters. The scenario with higher competition intensity for space in shallow habitats on sponge substrates combined with reduced survivorship of brachiopods is thus in accord with competitive superiority of bivalves and displacement of brachiopods to deep habitats with reduced competition for space.

High juvenile mortality of oysters – effects of competition for food? High juvenile mortality of cementing oysters in habitats dominated by brachiopods can be explained as combined effect of (1) low flow speeds and reduced food supply that did not support physiological requirements of cementing bivalves, and/or (2) as due to food depletion caused by brachiopods, implying that brachiopods were superior in exploitative competition for food (Fig. 28). Autochthonous and parautochthonous brachiopod shell beds in habitats below storm wave base provide evidence of high population densities and crowding. Crowding implicitly indicates space limitation and interference, although high population density does not always lead to reduced growth rates (Peterson, 1982). Dense populations of suspension-feeding bivalves may deplete food in the benthic boundary layer, especially under low flow speeds (Wildish and Kristmanson, 1984). Food depletion negatively affects downstream or small suspension-feeders close to sediment-water interface (Fréchette and Bourget, 1985; Kamermans, 1993; Ramón, 1996; Alunno-Bruscia et al., 2001; Lohse, 2002). Food depletion would thus be also limiting for juvenile cementing bivalves that settled in areas of dense brachiopod populations. High rates of biodeposition can also affect negatively neighboring suspension-feeders (Talman and Keough, 2001). It can be argued that brachiopods with low clearance rates and low metabolic rates with batch-feeding were less efficient in food depletion and biodeposition than present-day dense bivalve populations, and that bivalves were primarily inhibited by abiotic factors. However, food depletion caused by *dense* brachiopod populations represents an alternative scenario, which implies competitive superiority of brachiopods over bivalves under flow- and food-restriction. In any case, high-density brachiopod populations demonstrate their specific adaptations to flow- and food-limited conditions that inhibited cementing bivalves and/or their superior exploitation competitive ability with respect to other fauna under such conditions. Both alternatives are not in accord with the hypothesis that brachiopods were restricted to enemy-free habitats but rather indicate that brachiopods are specifically adapted for minimizing energy expenditure for maintenance and activity under flow-limited conditions owing to efficient filter-feeding and low metabolic rates (Pörtner et al., 2005). Similar reasoning was used by Okamura et al. (2001) in interpreting the ecology of bryozoans adapted to flow-limited environments.

Differences in population dynamics. Present-day dense populations of suspension-feeders are either controlled by variations in recruitment, or by variations in post-settlement mortality (Stillman et al., 2000; Van der Meer et al., 2001; Hills and Thomason, 2003). It seems that the origin of high-density brachiopod and bivalve beds of the Foum Zidet Formation was in generally related to these two distinct modes. Brachiopods achieved high shell density owing to substantially reduced mortality rates because their density positively correlated with high juvenile survivorship and high median adult size. Dm-scale brachiopod shell beds indicate that this state was not ephemeral and that they represent several overlapping generations with relatively stable densities and living near their carrying capacity. In contrast, thin concentrations of *Nanogyra* probably reflect short-lived patches resulting from massive recruitment because their shell density does not show any relationship to mortality and size patterns. *Nanogyra* may represent an opportunistic species with a high rate of increase in population size. Its population density was thus probably more influenced by recruitment variations. In addition to high growth rates, such a strategy might have been advantageous in habitats with high intensity of competition for space because *Nanogyra* was able to exploit a fresh substrate more rapidly than brachiopods owing to more frequent recruitment and dense settlement.

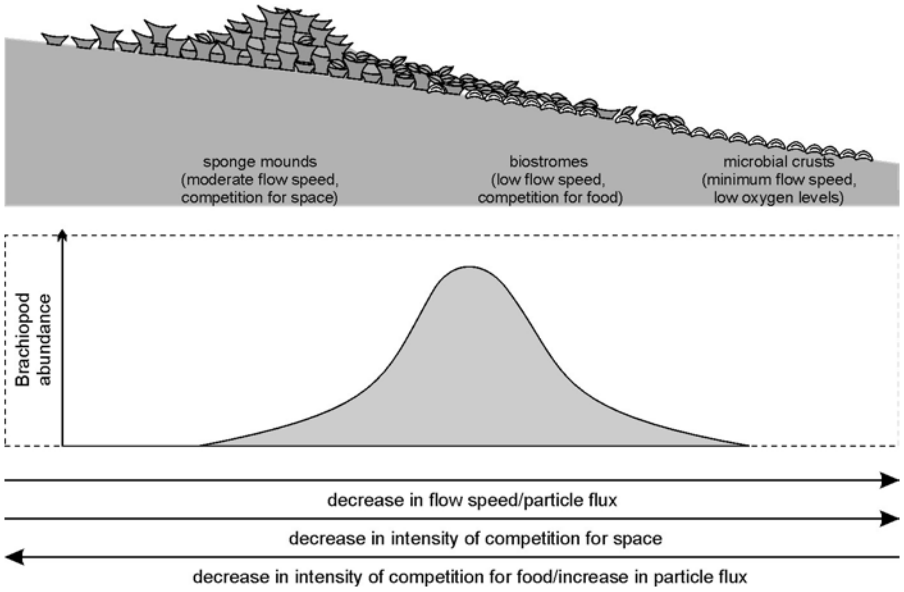


Figure 28 - Interpreted response curve of brachiopods to varying flow speed and competition intensity in sponge-microbial ecosystems.

Brachiopod dominance in sponge-microbial ecosystems – flow-limited food-acquisition hypothesis

Modern dense populations of sponges can have both positive and negative effects on other benthic organisms (Bett and Rice, 1992; Barthel et al., 1996; Gutt and Starmans, 1998). Dense sponge populations increase habitat heterogeneity, stabilize sediment and provide solid attachment substrate for larvae of other animals (Barthel, 1992, 1996; Gutt and Schickan, 1998; McClintock et al., 2005) and sponges have commonly commensalistic relationship with other benthic animals (Schiaparelli et al., 2003; Marin and Belluga, 2005). However, with increasing sponge density, intense interference competition for space can be induced by aggresive behaviour and overgrowth by sponges that are commonly superior competitors in space acquisition (Aerts, 1998; Hill, 1998; Kubanek et al., 2002). Allelopathic waterborne metabolites of sponges can also inhibit settlement of encrusters and epibionts (Dobretsov et al., 2004, 2005). On one hand, along a gradient with increasing sponge density, which might be related to a moderate increase in flow speeds (e.g., from biostromes to sponge mounds), brachiopods will be negatively affected by space-limitation. On the other hand, along a gradient with decreasing flow speeds, oxygen levels and increasing abundance of microbial crusts (e.g., up to purely thrombolithic deposits), brachiopods will be more limited by abiotically-induced resource limitation. It is thus suggested that the high abundance of brachiopods in sponge-microbial communities in general reflects combined effects of (1) a restricted flow regime, probably coupled with low light intensity and low oxygen levels limiting other competitors, and (2) the ability of brachiopods to acquire food effectively under flow-limited conditions. Brachiopod communities were probably characterized by low grazing disturbance and competition intensity for space, although abundance peaks of brachiopods leading to crowded life assemblages could also lead to resource limitation in such habitats. In addition, availability of stable, hard substrates in mixed-bottom habitats assured that brachiopods were not disturbed or did not compete for food with infaunal guilds. The predictions of this hypothesis are (1) a negative correlation between brachiopod abundance and abundance of encrusters and grazers, and (2) a decreasing abundance of bivalves and increasing abundance of brachiopods along decreasing flow speeds and particle flux in habitats with available hard substrates. In accord with this scenario, encrusting communities of Late Jurassic sponge-microbial communities were characterized by slow-growing heterotrophic animals (Schmid, 1996), and shallow-water encrusters and grazers such as echinoderms and gastropods were rare or absent. Sponge-microbial ecosystems with abundant brachiopods also invariably occur in low-energy, sheltered or deep habitats and commonly show signs of oxygen deficiency.

Conclusions

(1) Early Jurassic pedunculate brachiopods and cementing bivalves of the Foum Zidet Formation substantially differed in their environmental distribution. The oyster *Nanogyra* preferred shallow habitats above normal storm wave base with substrates formed by sponges and bioclasts. Brachiopods preferred deep habitats below maximum storm wave base with a substrate formed by microbial crusts and bioclasts. Multivariate analyses with a two-way crossed design indicate that *both* substrate and level of wave base had significant effects on abundances of brachiopods and bivalves. Two-way crossed analyses separating effects of time and substrate/habitat effects indicate that there was also a significant temporal within-habitat turnover caused by differential preferences of brachiopod genera. The overall wave-base level and substrate preferences of bivalves and brachiopods were constant in time. The differences in abundances of brachiopods and cementing bivalves were not related to substrate stability and sedimentation rate, which were rather constant through time, but

probably reflect combined effects of varying flow speed/particle flux and varying competition intensity for space and possibly also for food. Higher pumping and feeding rates of bivalves than brachiopods indicate that their differential distribution along a gradient with varying flow speeds reflects differences in their suspension-feeding strategies.

(2) Differential juvenile survivorship of brachiopods and bivalves among substrates, negative correlation between juvenile mortality rates of *Nanogyra* and abundance of adult pedunculate brachiopods, and negative correlation between juvenile mortality rates of the brachiopod *Zeilleria* and abundance of adult *Nanogyra* indicate that the ecology of juveniles had substantial effects on community-level abundance of brachiopods and bivalves. On one hand, cementing bivalves were able to thrive on sponge substrates with high intensity of competition for space in habitats with moderate flow speeds, either owing to their rapid growth rates or to a rapid population turnover leading to rapid exploitation of fresh substrates. Brachiopods with high juvenile mortalities were probably competitively inferior in such habitats. On the other hand, brachiopods were characterized by low juvenile mortality in habitats with reduced flow speeds and reduced intensity of competition for space. High juvenile mortality of *Nanogyra* in such habitats can be assigned to too low flow speeds, but high population densities of brachiopods indicate that *Nanogyra* might be also negatively affected by brachiopod-induced food depletion. Although competitive exclusion of brachiopods from shallow habitats with sponges is in accord with the escalation hypothesis (i.e., restriction of adaptively anachronistic brachiopods into enemy-free habitats), their abundance under flow-limited conditions indicates either specific adaptations to acquire food under flow-limited conditions and/or competitive superiority with respect to food exploitation under such conditions.

	FZ1-03	FZ1-04	FZ1-05	FZ1-07	FZ1-08	FZ1-12	FZ1-13	FZ1-15.6	FZ1-16	FZ1-17	FZ1-18	FZ1-20.2	FZ1-24.3	FZ1-26.3	FZ1-27	FZ1-27.2	FZ1-33	FZ1-34	FZ1-35	FZ1-36-1	FZ1-36-2	FZ1-38.2
Apodosia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atreta sp.	0	3	8	4	1	0	0	9	2	97	1	8	5	4	0	0	0	0	0	1	0	0
Chlamys sp. A	0	0	0	1	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Crania sp.	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0
Discinisca sp.	0	0	0	0	0	0	0	1	0	0	0	4	1	5	5	8	0	6	7	13	2	0
Dispiriferina sp.	0	12	53	0	2	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	4
Entolium sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gibbirhynchia moghrabiensis	2	7	25	3	0	27	28	79	11	18	39	0	0	0	0	0	0	0	0	0	0	0
Gibbirhynchia sp. A	0	0	1	0	1	0	0	7	6	0	8	0	0	0	0	0	0	0	0	0	0	0
Harpax sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Harpax sp. A	0	5	2	1	0	0	0	2	0	1	0	0	0	0	1	1	0	0	0	0	0	0
Liospiriferina rostrata	5	25	41	66	1	33	80	176	124	142	23	10	11	36	2	13	3	14	2	3	2	6
Modiolus sp.	0	4	0	0	0	0	0	9	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Moorellina sp.	7	106	229	152	59	0	69	0	0	0	0	0	0	0	0	1	0	0	0	0	0	15
Nanogyra nana	3	45	18	9	51	30	34	224	24	57	80	3	7	91	75	84	3	0	0	0	0	2
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	62	76	90	29	5
Grammatodon (C.) sp.	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma aff. *punctatum*	0	0	0	0	0	0	0	1	0	8	2	2	0	1	0	0	0	0	0	0	0	0
Plagiostoma sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	0	0	33	0	0	1	4	2	34	0	0	0	0	0	0	0	0	0	0
Prionorhynchia sp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	1	5	12	10	6
Pseudolimea sp.	0	0	0	0	0	0	0	3	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Pteria sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys sp. B	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0
Squamirhynchia sp. A	0	3	12	76	3	270	44	42	5	7	89	162	129	59	8	29	2	1	1	10	4	16
Squamirhynchia sp. B	0	0	0	0	0	0	0	95	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria rehmanni	0	0	0	0	0	0	0	0	0	0	0	0	0	51	1	6	10	30	63	41	29	45
Zeilleria sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria vicinalis	15	49	120	64	4	66	69	18	1	3	0	2	0	0	0	0	0	0	0	0	0	0
Koninckinid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Supplement 1 – Absolute abundances of brachiopod and bivalve taxa in the lower member of the Foum Zidet Formation.

	FZ1-40	FZ1-47	FZ3-7.3	FZ3-12.6	FZ3-12.7	FZ3-12.8	FZ3-13	FZ3-14	FZ3-14.7	FZ3-23.6	FZ3-23.8	FZ3-25	FZ3-28.2	FZ3-28.5	FZ3-30	FZ3-51	FZ7-40
Apodosia sp.	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
Atreta sp.	0	1	0	0	0	0	0	13	0	31	25	1	0	0	0	0	2
Chlamys sp. A	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Crania sp.	0	0	0	0	0	0	0	10	0	1	0	0	0	0	0	2	0
Discinisca sp.	2	1	0	0	1	1	0	0	0	1	18	8	0	8	2	0	2
Dispiriferina sp.	1	0	0	3	0	1	0	20	0	0	0	0	0	0	0	4	0
Entolium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Gibbirhynchia moghrabiensis	0	0	22	153	48	25	0	0	22	0	0	0	0	0	0	0	0
Gibbirhynchia sp. A	0	0	0	20	4	0	30	0	0	0	0	0	0	0	0	0	0
Harpax sp. B	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0
Harpax sp. A	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Liospiriferina rostrata	22	24	38	85	38	30	42	11	36	34	17	43	6	0	1	15	19
Modiolus sp.	0	0	0	1	0	1	0	0	4	0	0	0	0	0	0	0	0
Moorellina sp.	7	14	110	15	9	2	29	203	13	2	0	1	0	0	0	17	5
Nanogyra nana	1	0	0	45	12	6	6	58	343	0	46	31	11	58	3	24	1
Oxytoma sp.	2	10	0	0	0	0	0	3	0	0	0	0	1	0	7	49	4
Grammatodon (C.) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma aff. *punctatum*	0	0	0	0	0	0	0	4	0	1	0	0	0	0	0	0	0
Plagiostoma sp. A	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	12	5	1	0	0	0	11	12	0	0	0	0	0	1
Prionorhynchia sp.	3	5	0	0	1	0	0	0	0	0	0	2	8	1	1	3	2
Pseudolimea sp.	0	0	0	3	0	0	0	4	0	0	0	0	4	0	0	1	0
Pteria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys sp. B	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0
Squamirhynchia sp. A	7	24	1	168	27	9	1	7	30	54	60	25	0	2	0	11	13
Squamirhynchia sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria rehmanni	28	20	0	0	0	0	0	0	0	108	75	57	7	0	8	25	37
Zeilleria sp. A	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0
Zeilleria vicinalis	0	0	41	189	86	56	39	0	32	0	0	0	0	0	0	0	0
Koninckinid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) - Absolute abundances of brachiopod and bivalve taxa in the lower member of the Foum Zidet Formation.

Sample	Unit	Sample group	Substrate	Wave base
FZ1-03	1	*Zeilleria vicinalis-Moorellina*	microbial crusts	below MSWB
FZ1-04	1	*Zeilleria vicinalis-Moorellina*	sponge colonies	below NSWB
FZ1-05	1	*Zeilleria vicinalis-Moorellina*	microbial crusts	below MSWB
FZ1-07	1	*Zeilleria vicinalis-Moorellina*	microbial crusts	below MSWB
FZ1-08	2	*Moorellina-Nanogyra*	sponge colonies	below NSWB
FZ1-12	2	*Squamirhynchia*	sponge colonies	below MSWB
FZ1-13	2	*Zeilleria vicinalis-Moorellina*	sponge colonies	below MSWB
FZ1-15.6	3	*Nanogyra-Liospiriferina*	debris	above NSWB
FZ1-16	3	*Liospiriferina*	debris	above NSWB
FZ1-17	3	*Liospiriferina*	debris	above NSWB
FZ1-18	3	*Nanogyra-Liospiriferina*	microbial crusts	below NSWB
FZ1-20.2	3	*Squamirhynchia*	microbial crusts	below MSWB
FZ1-24.3	3	*Squamirhynchia*	sponge colonies	below MSWB
FZ1-26.3	4	*Nanogyra-Liospiriferina*	microbial crusts	below NSWB
FZ1-27	5	*Nanogyra*	sponge colonies	above NSWB
FZ1-27.2	5	*Nanogyra*	debris	above NSWB
FZ1-33	5	*Zeilleria rehmanni - Oxytoma*	debris	above NSWB
FZ1-34	6	*Zeilleria rehmanni - Oxytoma*	debris	below MSWB
FZ1-35	6	*Zeilleria rehmanni - Oxytoma*	debris	below MSWB
FZ1-36-1	6	*Zeilleria rehmanni - Oxytoma*	debris	below MSWB
FZ1-36-2	6	*Zeilleria rehmanni - Oxytoma*	debris	below MSWB
FZ1-38.2	7	*Zeilleria rehmanni*	microbial crusts	below MSWB
FZ1-40	7	*Zeilleria rehmanni*	microbial crusts	below MSWB
FZ1-47	7	*Zeilleria rehmanni*	microbial crusts	below MSWB
FZ3-7.3	1	*Zeilleria vicinalis-Moorellina*	microbial crusts	below MSWB
FZ3-12.6	2	*Zeilleria vicinalis-Moorellina*	debris	below NSWB
FZ3-12.7	2	*Zeilleria vicinalis-Moorellina*	debris	below NSWB
FZ3-12.8	2	*Zeilleria vicinalis-Moorellina*	debris	below NSWB
FZ3-13	2	*Zeilleria vicinalis-Moorellina*	microbial crusts	below MSWB
FZ3-14	2	*Moorellina-Nanogyra*	sponge colonies	below NSWB
FZ3-14.7	3	*Nanogyra*	sponge colonies	below NSWB
FZ3-23.6	4	*Zeilleria rehmanni*	microbial crusts	below MSWB
FZ3-23.8	4	*Zeilleria rehmanni*	microbial crusts	below NSWB
FZ3-25	4	*Zeilleria rehmanni*	microbial crusts	below NSWB
FZ3-28.2	5	*Nanogyra-Liospiriferina*	debris	above NSWB
FZ3-28.5	5	*Nanogyra*	debris	above NSWB
FZ3-30	5	*Zeilleria rehmanni - Oxytoma*	debris	below NSWB
FZ3-51	7	*Zeilleria rehmanni - Oxytoma*	debris	below NSWB
FZ7-40	7	*Zeilleria rehmanni*	microbial crusts	below MSWB

Supplement 2 – Environmental and stratigraphic assignments of 39 samples from the lower member of the Foum Zidet Formation.

Species	Guild
Apodosia sp.	pedunculate brachiopod
Atreta sp.	cementing filibranch
Chlamys sp. A	epibyssate filibranch
Crania sp.	cementing brachiopod
Discinisca sp.	pedunculate brachiopod
Dispiriferina sp.	pedunculate brachiopod
Entolium sp.	free-lying filibranch
Gibbirhynchia moghrabiensis	pedunculate brachiopod
Gibbirhynchia sp. A	pedunculate brachiopod
Harpax sp. B	cementing filibranch
Harpax sp. A	cementing filibranch
Liospiriferina rostrata	pedunculate brachiopod
Modiolus sp.	endobyssate filibranch
Moorellina sp.	cementing brachiopod
Nanogyra nana	cementing pseudolamellibranch
Oxytoma sp.	epibyssate filibranch
Grammatodon (Cosmetodon) sp.	epibyssate filibranch
Plagiostoma aff. *punctatum*	epibyssate filibranch
Plagiostoma sp. A	epibyssate filibranch
Plicatula sp.	cementing filibranch
Prionorhynchia sp.	pedunculate brachiopod
Pseudolimea sp.	epibyssate filibranch
Pteria sp.	epibyssate filibranch
Chlamys sp. B	epibyssate filibranch
Squamirhynchia sp. A	pedunculate brachiopod
Squamirhynchia sp. B	pedunculate brachiopod
Zeilleria rehmanni	pedunculate brachiopod
Zeilleria sp. A	pedunculate brachiopod
Zeilleria vicinalis	pedunculate brachiopod
Koninckinid sp.	pedunculate brachiopod

Supplement 3 - Guild assignments to 30 taxa of the Foum Zidet Formation

9. Ecology of brachiopods and bivalves (Middle Jurassic, Morocco): differential niche preferences along varying siliciclastic and food supply

(with Franz T. Fürsich)

Abstract. Brachiopods and bivalves inhabited mixed, siliciclastic-carbonate environments of the Central High Atlas Basin during the Early Bajocian, ranging from nearshore, high-energy oolite and skeletal bars, storm-influenced ramp with coral patch-reefs, up to offshore environments below maximum storm wave base. Analyses of similarities demonstrate that variations in wave-base level, substrate and siliciclastic supply had substantial effects on relative abundance of brachiopods and bivalves. Variations in wave-base level and substrate consistency had significant effects on guild abundances only in interaction with siliciclastic supply. The main effect of these two factors was an increase in abundance of infaunal bivalves and a decrease in abundance of cementing bivalves with decreasing substrate consistency and decreasing storm disturbance. Variations in siliciclastic supply showed significant effects on species and guild abundances even when storm disturbance and substrate were kept constant. Relative abundances of pedunculate brachiopods decreased and relative abundance of shallow burrowing bivalves increased with increasing rate of siliciclastic supply, indicating that differential niche preferences of brachiopods and bivalves were driven by varying rate of siliciclastic sedimentation. Shell density generally decreased with increasing depth and increasing siliciclastic supply towards the east in the Central High Atlas Basin. Marl and limestone beds derived from shallow habitats were characterized by higher shell density than those derived from deep habitats. Shell density negatively correlated with bed thickness of marls, indicating that higher net sedimentation rates controlled shell density via dilution or inhibition of shell producers. Poor differences in thickness among limestone beds differing in the shell density imply that the depth-related decrease in shell density of limestones was not governed by net sedimentation rate alone, but might be related to the decrease in food supply owing to reduced input of land-derived nutrients. Variations in relative abundances and shell density of brachiopods and bivalves are thus explained by combined effects of (1) sedimentation rate and particle concentrations that increased in magnitude during siliciclastic conditions, thus reducing abundance of brachiopods and overall shell density, and (2) food supply that decreased in abundance during carbonate-rich conditions, thus reducing abundance of shallow burrowing bivalves and overall shell density. This pattern is in accord with the hypothesis that pedunculate brachiopods and infaunal bivalves were characterized by partly segregated physical niches with respect to siliciclastic and food supply gradient.

Introduction

An analysis of evolutionary history of brachiopods and bivalves in ecologic terms should involve tracing their possible niche overlaps and segregations through time with respect to main environmental factors that limited their niches. Niche overlap along some resource gradient might indicate that two taxa were in competition but it can also follow when the resource was not in short supply or the taxa were separated along other resource axes (Pianka, 1994). Niche segregation can indicate that the two taxa competitively interacted in the past and evolved distinct habitat preferences by reducing their niche overlap, or differences in resource utilization can result from other historical or phylogenetic processes unrelated to competitive exclusion (Gotelli and Graves, 1996). Although niche overlap and segregation can thus originate by various pathways, changes in niche preferences of brachiopods and bivalves through time may indicate whether the decrease in brachiopod abundance can be related to their niche reduction owing to niche expansion of bivalves, or whether the niches of brachiopods and bivalves were segregated through time. Environmental factors determining differences in distribution of brachiopods and bivalves in marine habitats were mainly related to their requirements with respect to substrate, wave exposure, bottom current velocity, sedimentation rate, turbidity, quality and quantity of food supply, oxygen concentrations, competition ability and predation resistance (Steele-Petrović, 1979; Richardson, 1981; James et al., 1992). Therefore, variations in these factors can be used for evaluating and quantifying of niche preferences of brachiopods and bivalves.

Richardson (1997) argued that present-day brachiopods are primarily substrate-controlled and substrate-limitation of brachiopods was also documented in fossil assemblages (Fürsich 1976; Fürsich et al. 1991, 2004a, b; Aberhan, 1992; Garcia and Dromart, 1997; Gahr, 2005). Richardson (1997) also suggested that very high depth and latitudinal tolerances of present-day brachiopod species imply that food supply, temperature and water energy are unlikely to be the factors controlling their distribution. This idea contrasts with the studies that showed that Paleozoic and Mesozoic brachiopods possessed unique bathymetric preferences (Fürsich and Hurst, 1974; Patzkowsky, 1995; Holland et al., 2001). In addition, it also contrasts with the findings that variations in siliciclastic/carbonate supply and food supply had substantial effects on distribution and abundance of fossil brachiopods (Fürsich et al., 2001). Kowalewski et al. (2002) suggested that the contrast between tolerances of fossil and present-day brachiopods may reflect real differences in preferences of particular brachiopod clades, or it can represent some profound temporal change in ecology of benthic communities. However, high tolerances of present-day brachiopod species along bathymetric and food supply gradients are mutually not exclusive with the idea that these factors substantially influence their abundance. First, the tolerances can be relatively high but quantitative analyses have to be performed to show that the environmental factors have *no* effects on brachiopod distribution patterns. Second, various environmental factors do not influence abundance patterns independently, but their effects interact so that abundance variations along a gradient of one factor depend also on other factors (Krebs, 1999). Therefore, testing whether variations in depth and food supply indeed determine distribution patterns of brachiopods has to control for variation in other factors that can substantially affect brachiopod ecology.

To test effects of siliciclastic and food supply and to infer relationships between physical niches of the Middle Jurassic (Bajocian) brachiopods and bivalves, their relative abundance patterns in a mixed, carbonate-siliciclastic environment of the Central High Atlas intra-shelf basin (Morocco, Fig. 1A) are linked to variations in three environmental factors. To evaluate whether shell density was mainly driven by varying sedimentation rates, variations in shell density are compared with depth-related trends in thickness of limestones and marls. The Middle Jurassic deposits of the Morocco are known to be rich in brachiopods and bivalves (Termier, 1936; Gardet and Gérard, 1946; Colo, 1961; Rousselle, 1964, 1965, 1967; Rousselle and Chavanon, 1981). The partitioning of the Lower Bajocian deposits of the Central High Atlas Basin into carbonate and siliciclastic-dominated stratigraphic intervals is essential for addressing differential effects of sediment and food supply on ecology of brachiopod and bivalves.

Three environmental factors include variations in (1) carbonate vs. siliciclastic supply, which can reflect sedimentation rates, turbidity and land-derived nutrient supply, (2) substrate consistency, and (3) water energy, which is related to a position of depth-dependent fair-weather and storm wave base. Although other factors such as light and temperature are not directly controlled, they should predictably change with variations in sedimentation regime and depth. An initial hypothesis based on differences in distribution patterns, physiology and suspension-feeding of present-day brachiopods and bivalves (Rhodes and Thompson, 1992, 1993) implies that brachiopods are well adapted to habitats with reduced food supply and reduced particle concentrations and eulamellibranch bivalves are well adapted to habitats with abundant food supply and high turbidity levels. Filibranch and pseudolamellibranch bivalves can probably cope with varying food supply and turbidity levels. To test this hypothesis about differential preferences of brachiopods and eulamellibranch bivalves with respect to sedimentation and food supply, it is important to control for substrate parameters because epifaunal brachiopods and eulamellibranch, mainly infaunal bivalves are expected to prefer substrates with different consistency.

To assess whether brachiopods and bivalves differed in their niche preferences, differences in abundances among brachiopods and bivalves, and specifically among brachiopods and eulamellibranch bivalves are quantified by an R statistic, which follows from R-mode analysis of similarities (ANOSIM). Q-mode ANOSIM is used to test the effects of these factors on community composition and. In addition to one-way analyses that evaluate whether there are any differences in community composition among groups of one factor (e.g., siliciclastic supply), two-way analyses are used to test these differences with another factor being constant (e.g., depth). Finally, to evaluate differences in community composition among groups of one factor (e.g., siliciclastic supply) and to keep other two factors constant (i.e., depth and substrate), two-way analyses were restricted to one substrate type (e.g., two-way ANOSIM evaluating effects of siliciclastic supply and depth *within* soft-bottom habitats).

Setting

During the Middle Jurassic, the Central High Atlas Basin (CHARB) was a relatively long and narrow embayment on the southeastern margin of the Tethys Ocean (Stanley, 1981; Beauchamp et al., 1999). The depositional environments of the CHARB during the Bajocian were influenced by a renewed extension phase that took place during the Toarcian, leading to disintegration of the Pliensbachian carbonate platform (Laville et al., 2004). In addition to a basin-scale increase in water depth towards central parts of the CHARB, the sedimentation during the Bajocian was substantially influenced by transcurrent, synsedimentary faults (Löwner et al., 2002), and by siliciclastic input that was probably derived from the southern margin of the basin. During the Early Bajocian, peritidal flats in the western and southwestern parts of the CHARB were replaced towards the east and north by ooidal, oncoidal and skeletal bars, and coral patch-reefs that formed a margin of the carbonate platform and belong to the Bin El Ouidane Formation (Fig. 2; Alméras et al., 1994; Milhi et al., 2002). These marginal deposits formed a rim also along the northern side of the CHARB. They gradually passed into the basin, probably without a substantial platform-margin break. The central part of the CHARB was formed by the Agoudim Formation that was represented by soft-bottom carbonate and siliciclastic muds, and locally also by coral pinnacle- and patch-reefs.

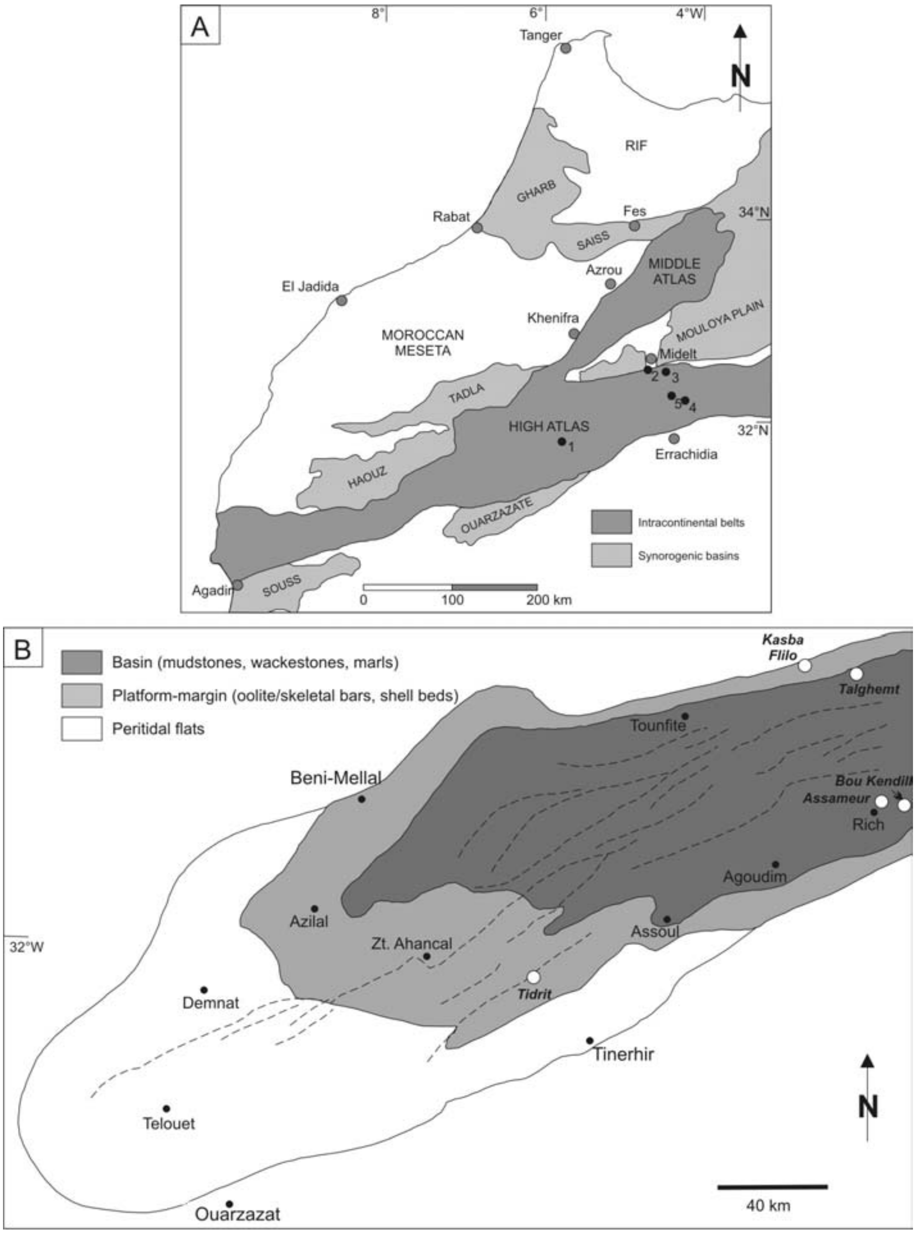


Figure 1 - A. Simplified tectonic map of Morocco showing the position of five sections in the High Atlas (after Arboleya et al., 2004). B. Simplified paleogeographic map of the Central High Atlas showing depositional environments and position of five sections (after Milhi et al., 2002).

Macrobenthic assemblages were sampled in five sections of the Bajocian age (Fig. 3). One section (Tidrit, Fig. 4) is situated in the southwestern part of the Central High Atlas, and four sections (Kasba Flilo, Talghemt, Bou Kendill and Assameur) are situated in the northeastern and eastern part of the Central High Atlas. The Tidrit section is formed by the Bin El Ouidane Formation (Fig. 2) that consists of three members (Fig. 4, Monbaron, 1981; Hauptmann, 1990; Milhi, 1992; Souhel, 1996). The Bin El Ouidane Formation is comparable to the R`cifa Formation in the Middle Atlas (Termier, 1936; Dresnay, 1963). Four sections in the eastern part of the Central High Atlas (Fig. 1B) expose the uppermost parts of the Agoudim Formation (Fig. 2). The Talghemt (Fig. 5) and Kasba Flilo (Fig. 6) sections were situated closely to the northeastern margin of the basin (Sadki, 1996). The Bou Kendill (Fig. 7) and Assameur (Fig. 8) sections in the Rich area were situated in the centre of the CHARB (Stanley, 1981; Sadki and Alméras, 1992; Sadki, 1992, 1996; Alméras et al., 1994). The Agoudim

Formation consists of alternation of several meters thick marl intervals with dm-scale thick limestone intervals. This formation is relatively abruptly replaced by an about 50 m-thick succession of coral limestones that form marked, several meters thick pinnacle- and patch-reefs.

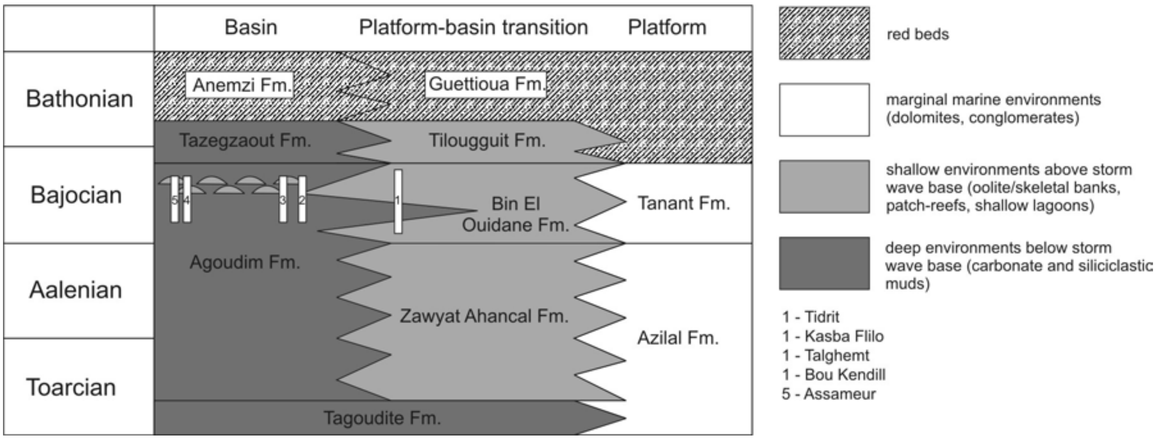


Figure 2 - Simplified lithostratigraphic scheme of the Middle Jurassic of the Central High Atlas (after Milhi et al., 2002) and the stratigraphic position of five sections.

Sections

Tidrit. This section situated approximately 50 km NE of Boulmane du Dades represents the platform-basin transition in the southwestern part of the CHARB (Milhi, 1992). The lower and upper members of the Bin El Ouidane Formation are formed by aggrading and prograding oolite and bioclastic skeletal bars, locally with small-scale coral patch-reefs and fine-grained deposits (Figs. 3, 4, 9A). In the lower member, laminated mudstones, thin packstones/grainstones and marls with shelly pavements in the lower parts are replaced by 5 to 10 meters thick, cross-bedded oolite bars in the upper parts. Thick oolite bars alternate with 0.5 to 2 meters thick marls that contain densely/loosely packed and moderately sorted concentrations of brachiopods, oysters and corals in lowermost and uppermost parts. The middle parts of marls contain dispersed shells of infaunal bivalves. Therefore, shell density is distributed relatively symmetrically within marls in the lower member of the Bin El Ouidane Formation. Locally, oolite beds truncate marls and shell concentrations are then mainly preserved in lowermost parts of marls.

The middle member of the Bin El Ouidane Formation is about 60 meters thick and consists of alternation of several meters thick marls with meter-scale intervals rich in limestone beds (Figs. 3, 4, 9B). Limestone beds in the middle member are commonly characterized by loosely and densely packed floatstones and rudstones with brachiopod (*Rhactorhynchia, Stiphrothyris*). The rhynchonellid brachiopod *Rhactorhynchia* forms clusters of articulated shells embedded in moderately sorted packstones and rudstones with concordantly oriented bioclasts in the upper parts of the middle member (Fig. 10A-B). Some shell concentrations were also dominated by epifaunal bivalves (*Liostrea, Rostroperna,* Fig. 10C). Coral debris and small-scale coral patch-reefs are locally also present. Limestone beds vary in taphonomic preservation, packing, sorting, preferred orientation of shells and internal structure. They mainly represent storm-reworked, single- or multiple-event shell concentrations. Marls in the middle member contain mainly dispersed bivalve shells, thin pavements or cm-scale layers with winnowed shell concentrations dominated by *Nicaniella*.

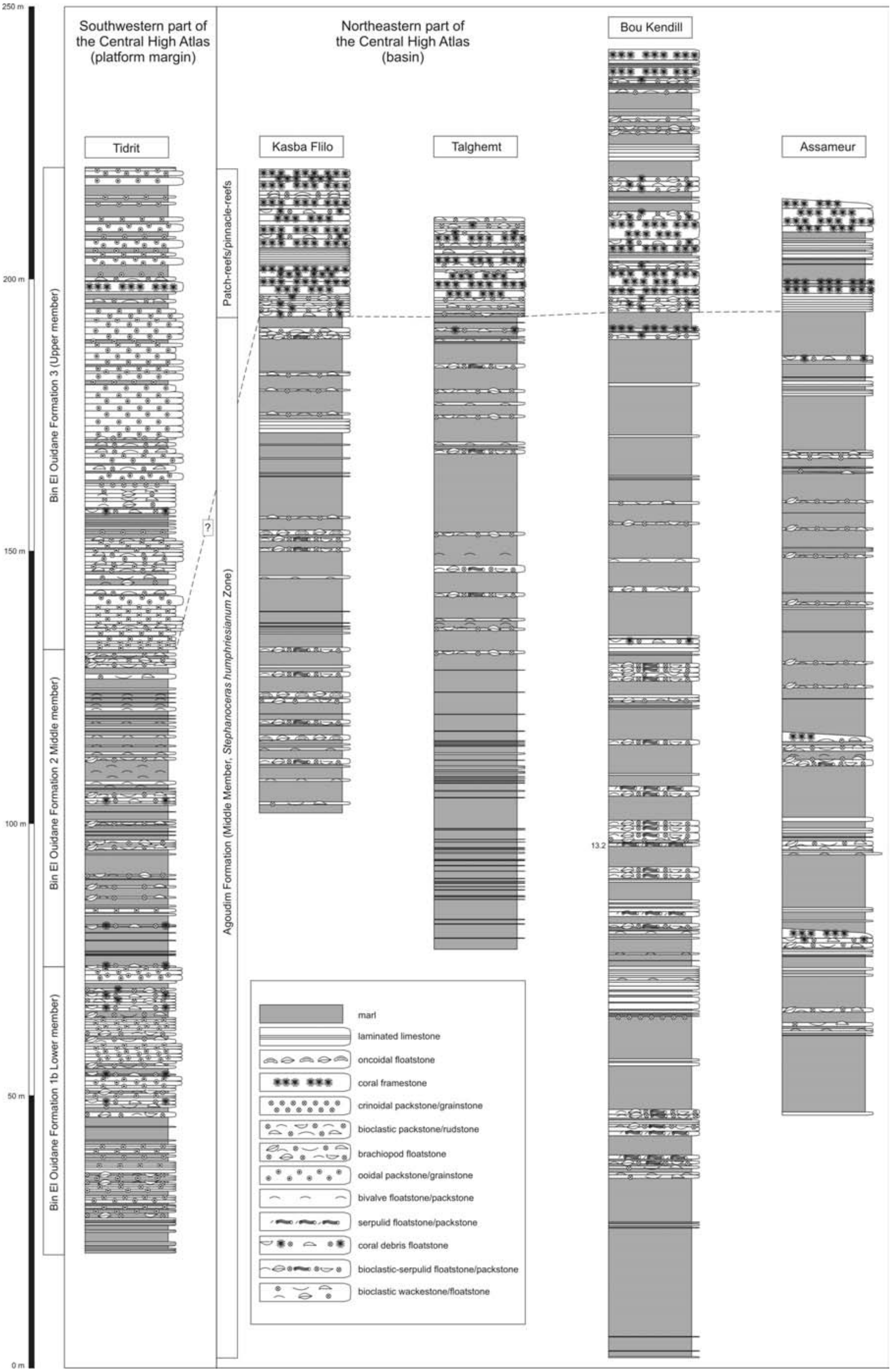


Figure 3 - Five sections showing temporal variations in sedimentologic features of the Bajocian deposits and their lithostratigraphic subdivision.

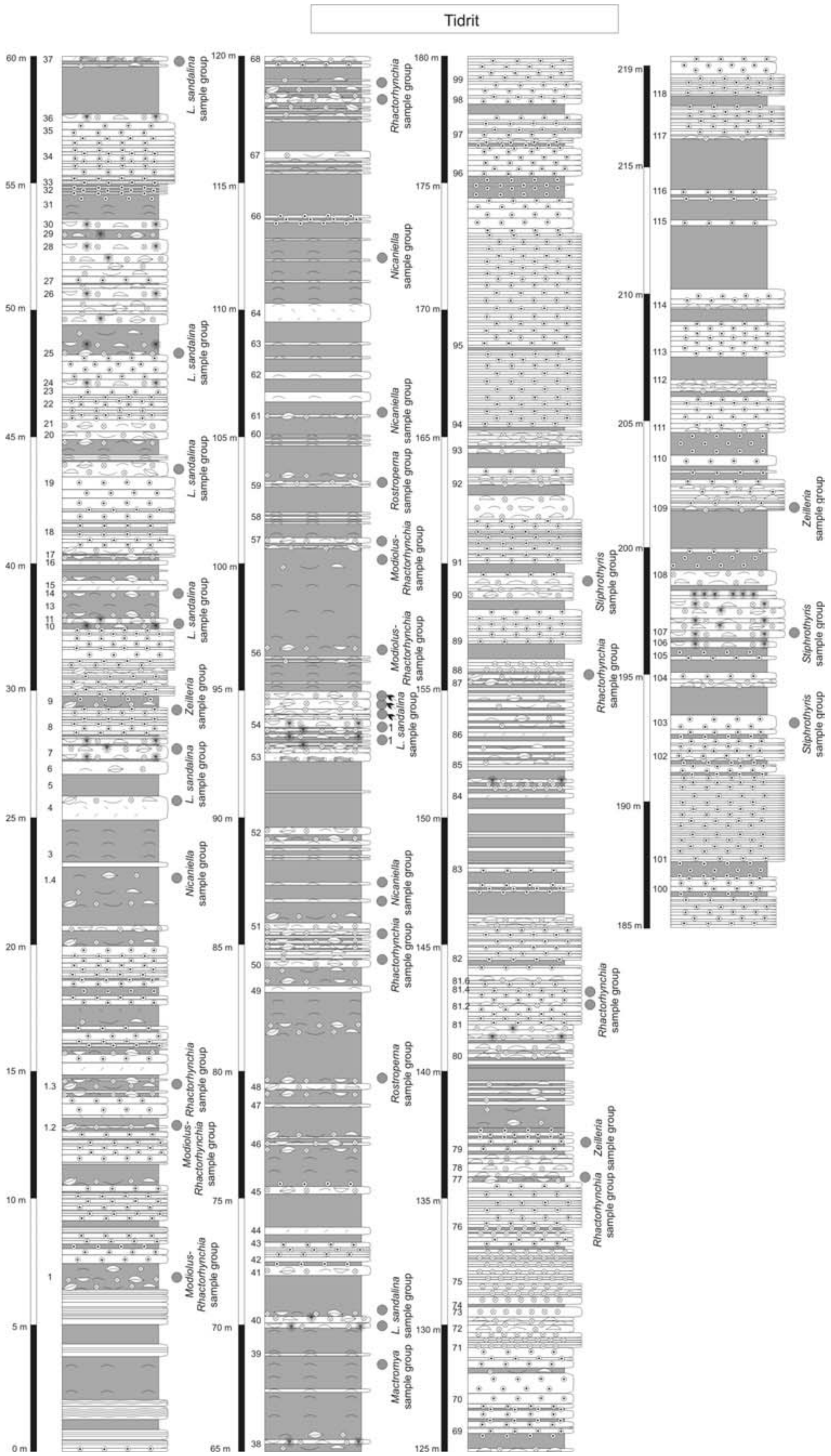


Figure 4 - Stratigraphic distribution of sample groups in the Bin El Ouidane Formation (Lower Bajocian) at Tidrit. Oolite bars occur in the lower and upper members. An alternation of meter-scale marls and dm-scale shell beds is typical of the middle member of the Bin El Ouidane Formation. Note: 1 – *Stiphrothyris* sample group. Lithologic explanations: see Fig. 6.

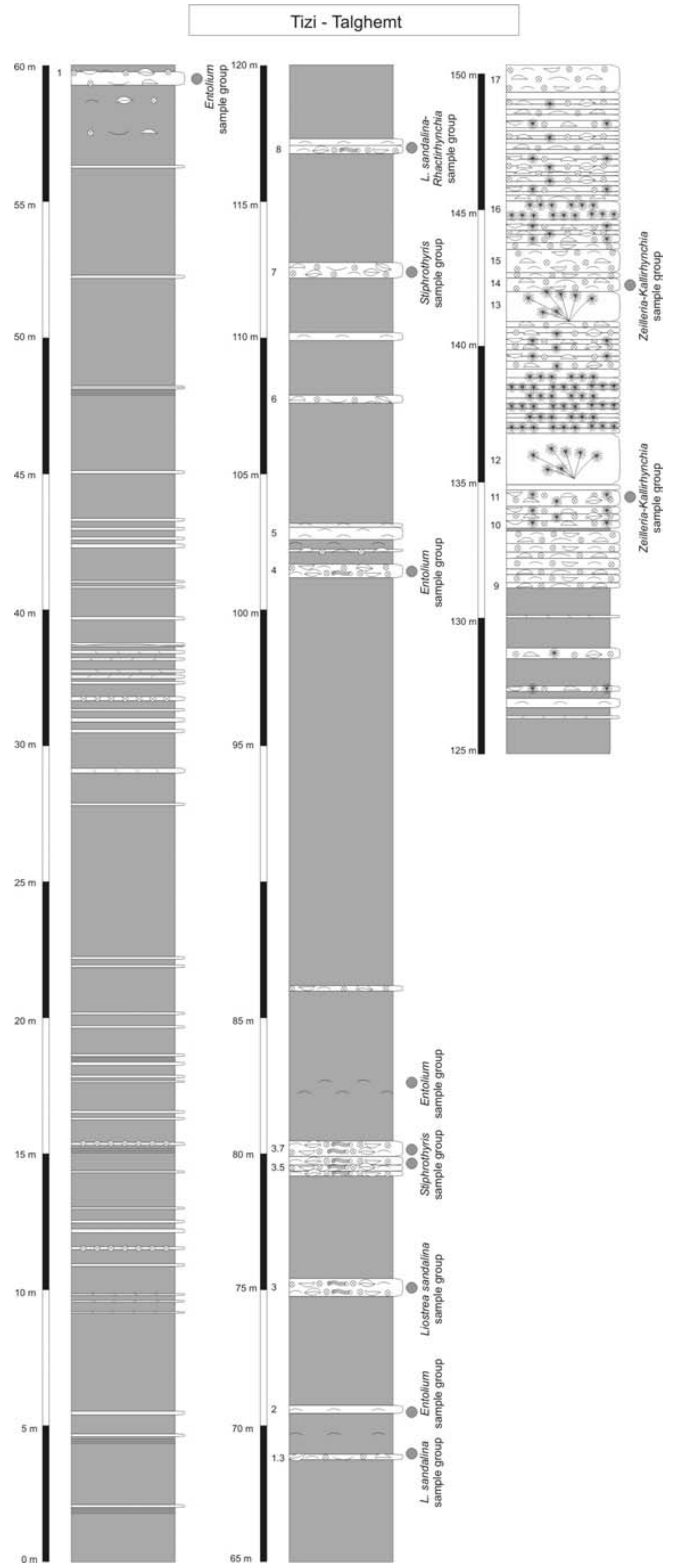


Figure 5 - Stratigraphic distribution of sample groups in the upper part of the Agoudim Formation and in the overlying carbonate-rich coral patch-reefs (Lower Bajocian) at Talghemt. Note the high abundance of aggregated serpulids *Filograna socialis* in the Agoudim Formation. Lithologic explanations: see Fig. 6.

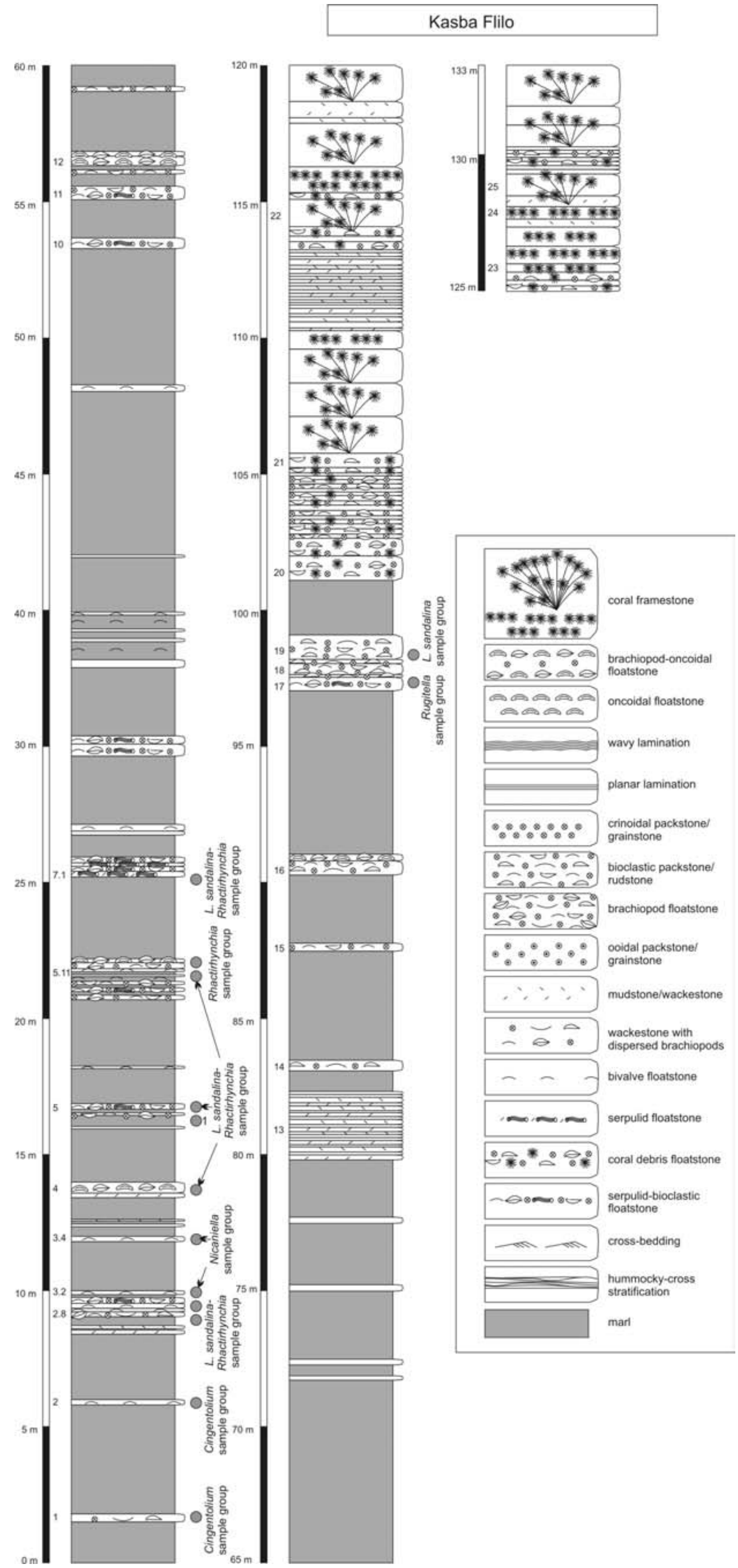


Figure 6 - Stratigraphic distribution of sample groups in the upper part of the Agoudim Formation and in the overlying carbonate-rich coral patch-reefs (Lower Bajocian) at Kasba Flilo. Note the high abundance of aggregated serpulids *Filograna socialis* in the Agoudim Formation. Note: 1 – *Entolium* sample group.

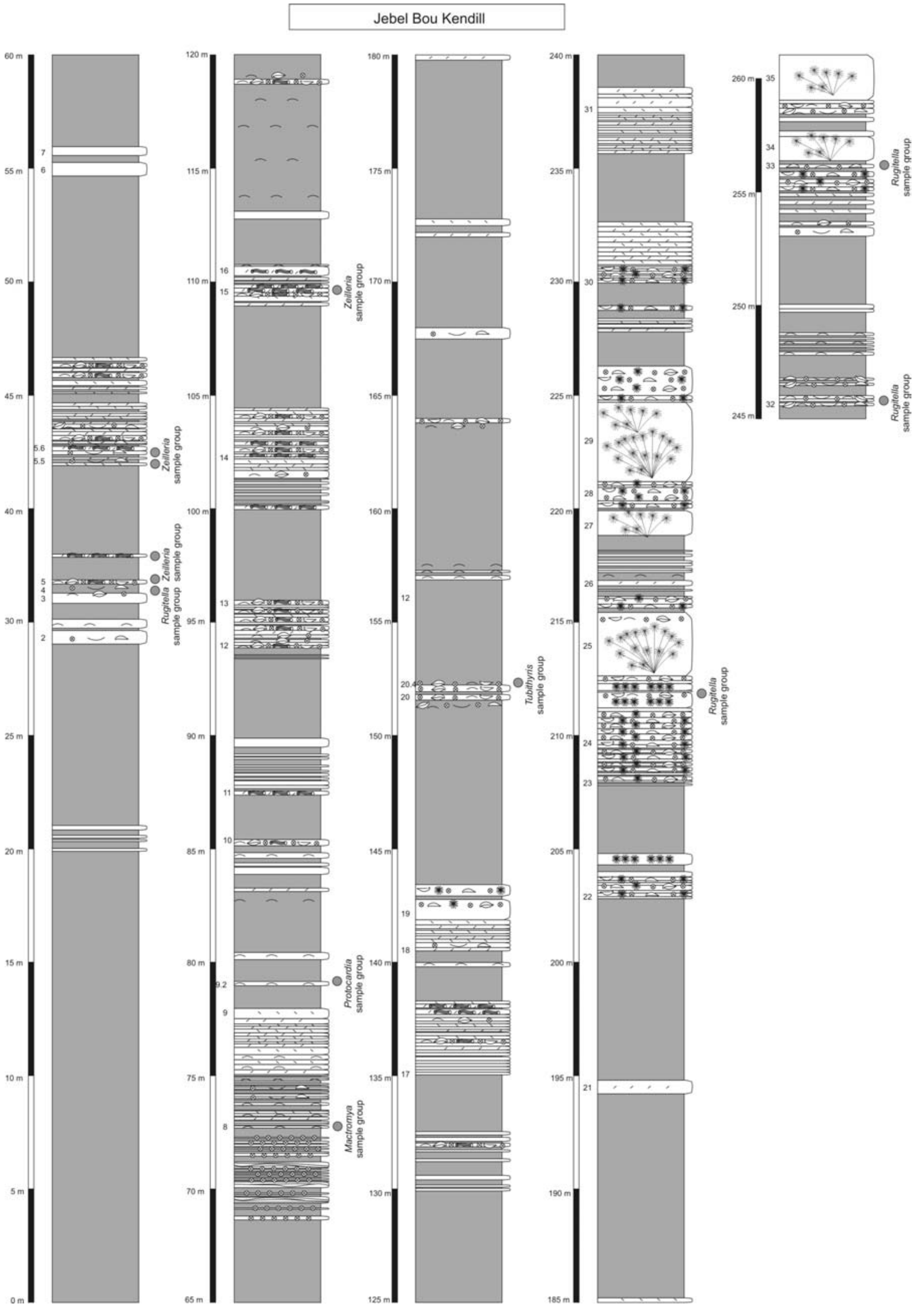


Figure 7 - Stratigraphic distribution of sample groups in the upper part of the Agoudim Formation and in the overlying carbonate-rich coral patch-reefs (Lower Bajocian) at Jebel Bou Kendill (southern part). This section occurs in the central part of the Central High Atlas Basin. Lithologic explanations: see Fig. 6.

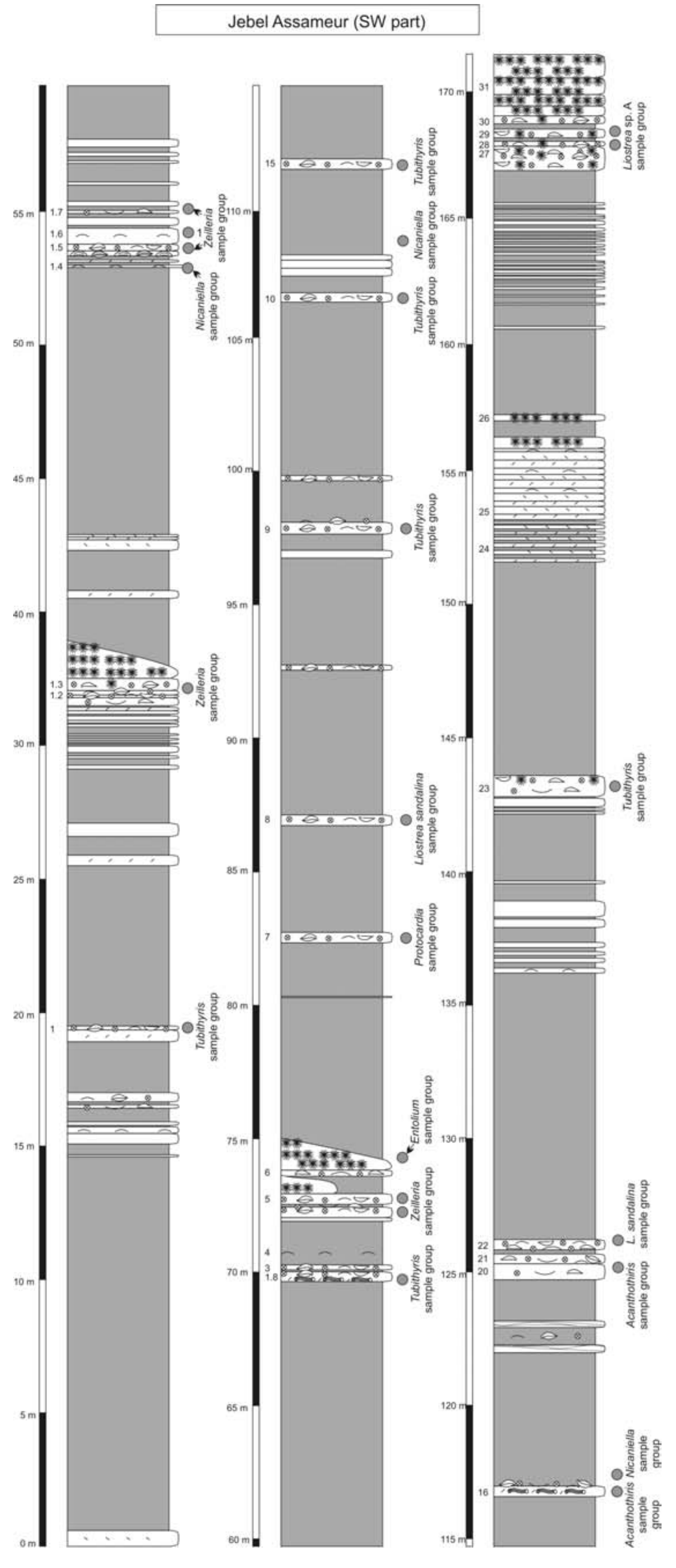


Figure 8 - Stratigraphic distribution of sample groups in the upper part of the Agoudim Formation and in the overlying carbonate-rich coral patch-reefs (Lower Bajocian) at Jebel Assameur (southeastern part). This section occurs in the central part of the Central High Atlas Basin. Note: 1 – *Mactromya* sample group. Lithologic explanations: see Fig. 6.

Several marls are characterized by dense, highly diverse concentrations of well preserved bivalve and brachiopod shells (e.g., *Rhactorhynchia, Modiolus, Mactromyopsis, Liostrea, Actinostreon*), especially in the middle parts of the middle member (Fig. 10D). In comparison to other marls, they represent combined effects of high rate of shell production and reduced net rate of sedimentation. Brachiopods are generally rare in marls, in contrast to infaunal bivalves (*Nicaniella, Mactromya*). Similarly as in the lower member, shell density within marls is mostly symmetrically distributed, with the highest shell density being present in their lowermost and uppermost parts near boundaries with limestone-rich intervals.

Oolite bars of the upper member (Fig. 9C) contain well sorted and densely packed pavements with disarticulated and concordant terebratulid valves (Fig. 10E). Some cross-bedded packstones and grainstones enclose dm-scale clusters and nests, or 10 cm-thick rudstone lenses with densely packed rhynchonellids *Rhactorhynchia* filled with cement (Fig. 10F). These shell concentrations are either characterized by high proportions of randomly oriented articulated shells, or by abundance of fragmented valves in stacked, nested or edgewise orientations. Oolite bars with abundant rhynchonellids in the comparable stratigraphic levels in the Beni-Mellal area had been termed as "Barre à Rhynchonelles" by Rolley (1978).

Talghemt. This section was described by Sadki (1996, section TT2). The section through the upper parts of the Agoudim Formation is about 100 meters long (Figs. 3, 5). Thin laminated packstones occur in the lower parts of the Agoudim Formation. Marls contain rare bivalves (*Entolium*). Limestone beds in the upper parts of the Agoudim Formation are represented by shell-rich floatstones and packstones with terebratulid brachiopods (*Stiphrothyris*), epifaunal bivalves (*Liostrea, Entolium*) and oncoids. They are characterized by mass occurrences of serpulid aggregations (*Filograna socialis*). They show complex internal structure and signs of moderate sorting, although signs of amalgamation are missing. The coral patch-reefs that overlie the Agoudim Formation are formed mainly by framestones and floatstones with massive, highly bored corals, and by skeletal-intraclastic rudstones and packstones with rhynchonellids (*Kallirhynchia*) and terebratulids (*Zeilleria*).

Kasba Flilo. This section was described by Alméras and Sadki (1992) and Sadki (1996). An about 90 m-thick part of the Agoudim Formation is shown in Figures 3, 6 and 9D. This part was termed as "Couches du Flilo" by Sadki (1996). Similarly as in the Talghemt section, marls contain rare bivalves and limestone beds are mainly represented by shell-rich floatstones and packstones. Limestone beds in the lower parts are dominated by the free-lying bivalve *Entolium (Cingentolium)* sp. Higher, the multicostate rhynchonellid *Rhactorhynchia* and the cementing oyster *Liostrea sandalina* and *Nanogyra nana* are abundant in floatstones with serpulid aggregations (*Filograna asocialis*). [Note that the rhynchonellid genus was assigned to *Burmirhynchia* by Alméras and Sadki (1992)]. Marly limestones are dominated by the shallow burrwoing bivalve *Nicaniella*. Limestone beds in the middle and upper parts of the Agoudim Formation are characterized by lower shell density. In the upper parts, a 2 m-thick shell-rich interval consisting of floatstones and rudstones dominated by the terebratulid brachiopod *Rugitella* is present. The coral patch-reefs that overlie the Agoudim Formation are formed by framestones with branching corals.

Bou Kendill. The Aalenian-Lower Bajocian section up to the *Otoites sauzei* Zone at Bou Kendill was described by Sadki (1992, 1996) and Alméras et al. (1994). The *Otoites sauzei* Zone is mainly characterized by alternation of thick marls with thin marly mudstones and rare benthic fauna (Sadki, 1996). It also contains two marked, 70-80 cm-thick skeletal bank rich in ooids, intraclasts, and crinoidal, brachiopod and bivalve debris (beds 77 and 95 in Sadki, 1996). The lower skeletal bank is dominated by the rhynchonellid brachiopod *Rhactorhynchia*. Higher, the Agoudim Formation (Fig. 7) consists of thick marls with rare bioclasts and limestone beds that are locally rich in brachiopods (*Zeilleria*) and serpulid aggregations (*Filograna socialis*). The proportion of limestone beds with high shell density is lower in comparison to the Tridrit, Talghemt and Kasba Flilo sections. The upper parts of some marl intervals are characterized by presence of well sorted, laminated and hummocky-cross stratified packstones and grainstones with silt and sandy admixture. In the upper part, limestone beds in the Agoudim Formation are generally shell-poor. The Agoudim Formation is overlain by patch-reefs formed by framestones with branching corals. The terebratulid brachiopod *Rugitella* occurs either among coral branches or is preserved in floatstones that occur between coral patch-reefs.

Assameur. Several sections through the Jebel Assameur were described by Stanley (1981). The section shown in Figures 2 and 8 was sampled along the SW margin of the Jebel Assameur (Fig. 9E). Limestone beds in the lower part of the section are formed by wackestones or floatstones with dispersed or loosely packed brachiopods (*Zeilleria*), bivalves (*Entolium*) and serpulids (*Filograna*). In two cases, a 40-45 cm-thick beds pass laterally into a 2-3 m-thick coral framestones with highly bored and encrusted corals. These small-scale patch-reefs are about 10-20 m in lateral extent and are stratigraphically onlapped by marls (Fig. 9F). Similarly as in the Bou Kendill section, limestone beds in the middle parts of the Assameur section are shell-poor. Limestone beds in the middle parts of the section contain cm-scale pavements with well preserved concentrations of the terebratulid *Tubithyris* at their top. Marl intervals are invariably characterized by rare or dispersed bivalves (*Nicaniella*). The shell density is locally higher in the lower parts of marl intervals. Therefore, shell density is rather asymmetrically distributed within marl-limestone sequences in the middle parts of the section, with the highest shell density being attained near the upper boundary of limestone beds. Coral patch-reefs above the Agoudim Formation consist of framestones that alternate with marls and rhythmically bedded mudstones.

Stratigraphy

The age of the Bin El Ouidane Formation is poorly constrained (Hauptmann, 1990; Milhi, 1992). The foraminifer *Timidonella sarda* in the lower member may point to the *Otoites sauzei* Zone (Souhel, 1996), and brachiopods in the upper parts might indicate a boundary between the Lower and Middle Bajocian. The uppermost parts of the Agoudim Formation just below the coral patch-reefs in the Kasba Flilo section correspond to three subzones of the *Stephanoceras humphriesianum* Zone (late Early Bajocian, Alméras and Sadki, 1992; Sadki, 1996). Similarly, the upper parts of the Agoudim Formation belong to the *S. humphriesianum* Zone in the Talghemt section (Sadki, 1996). In the Bou Kendil section, the *Otoites sauzei* Zone reaches approximately up to an about 100 cm-thick, cross-bedded bioclastic-intraclastic limestone (Sadki, 1996), which is present at the base of the section analyzed in this chapter. Therefore, it is assumed that an about 200 m-thick part of the Agoudim Formation formed by alteration of marls with limestone beds below the coral patch-reefs in the Kasba Flilo, Talghemt, Bou Kendill and Assameur sections corresponds to the *Stephanoceras humphriesianum* Zone. The age of the coral patch-reefs is not constrained in the Central High Atlas. Any signs of extensive condensation are missing and the reefs may correspond to the Lower/Upper Bajocian boundary (Alméras and Sadki, 1992). In the Middle Atlas, upper parts of the R`cifa Formation also correspond to the uppermost parts of the *S. humphriesianum* Zone (Dresnay, 1963). In this study, the lower member of the Bin El Ouidane Formation is preliminarily correlated with skeletal and ooidal banks within the Agoudim Formation at the base of the Bou Kendill section. These banks were dated as the uppermost parts of the *O. sauzei* Zone (Sadki, 1996). The middle member of the Bin El Ouidane Formation is preliminary correlated with the uppermost parts of the Agoudim Formation (*S. humphriesianum* Zone). The succession of coral limestones overlying the Agoudim Formation is correlated with the upper member of the Bin El Ouidane Formation (Lower/Upper Bajocian).

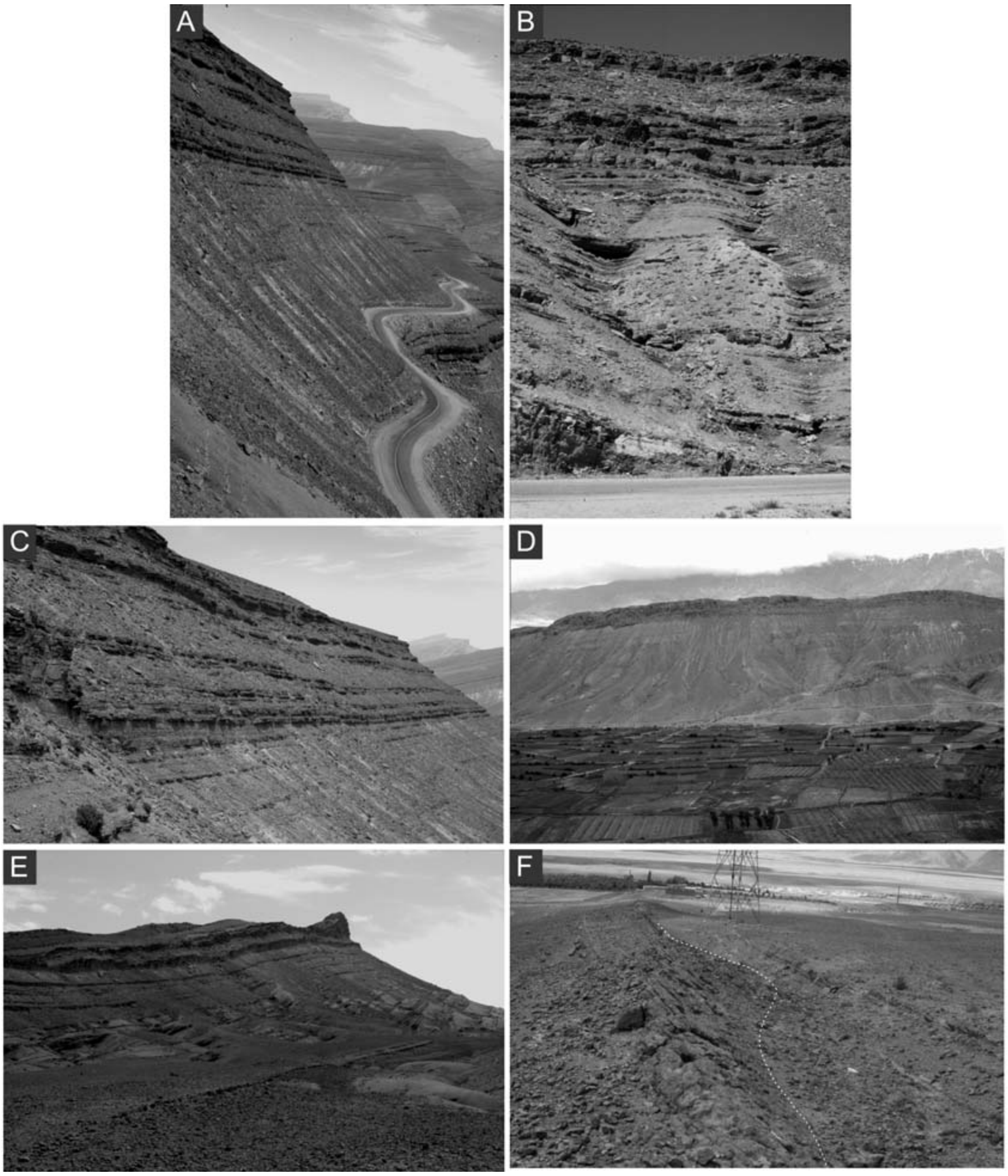


Figure 9 - A. An about 150 m-thick succession exposes the middle and upper members of the Bin El Ouidane Formation in the Tidrit section. B. Close-up of the middle member of the Bin El Ouidane Formation that consists of meter-scale soft and friable marls and dm-scale bioclastic limestones that form marked ridges. C. Close-up of the upper member of the Bin El Ouidane Formation that consists of meter-scale oolite and skeletal bars. D. The upper part of the siliciclastic-rich Agoudim Formation capped by a carbonate-rich interval with coral-patch-reefs in the Kasba Flilo section. E. The upper part of the siliciclastic-rich Agoudim Formation in the Assameur section. It consists of several meters thick marls that alternate with markedly weathering, dm-scale mudstones and floatstones. The formation is capped by coral patch-reefs or pinnacle-reefs. F. An about 45 cm-thick floatstone within the Agoudim Formation is laterally replaced by a 2.5 m-thick patch-reef formed by coral framestones and floatstones (Assameur section).

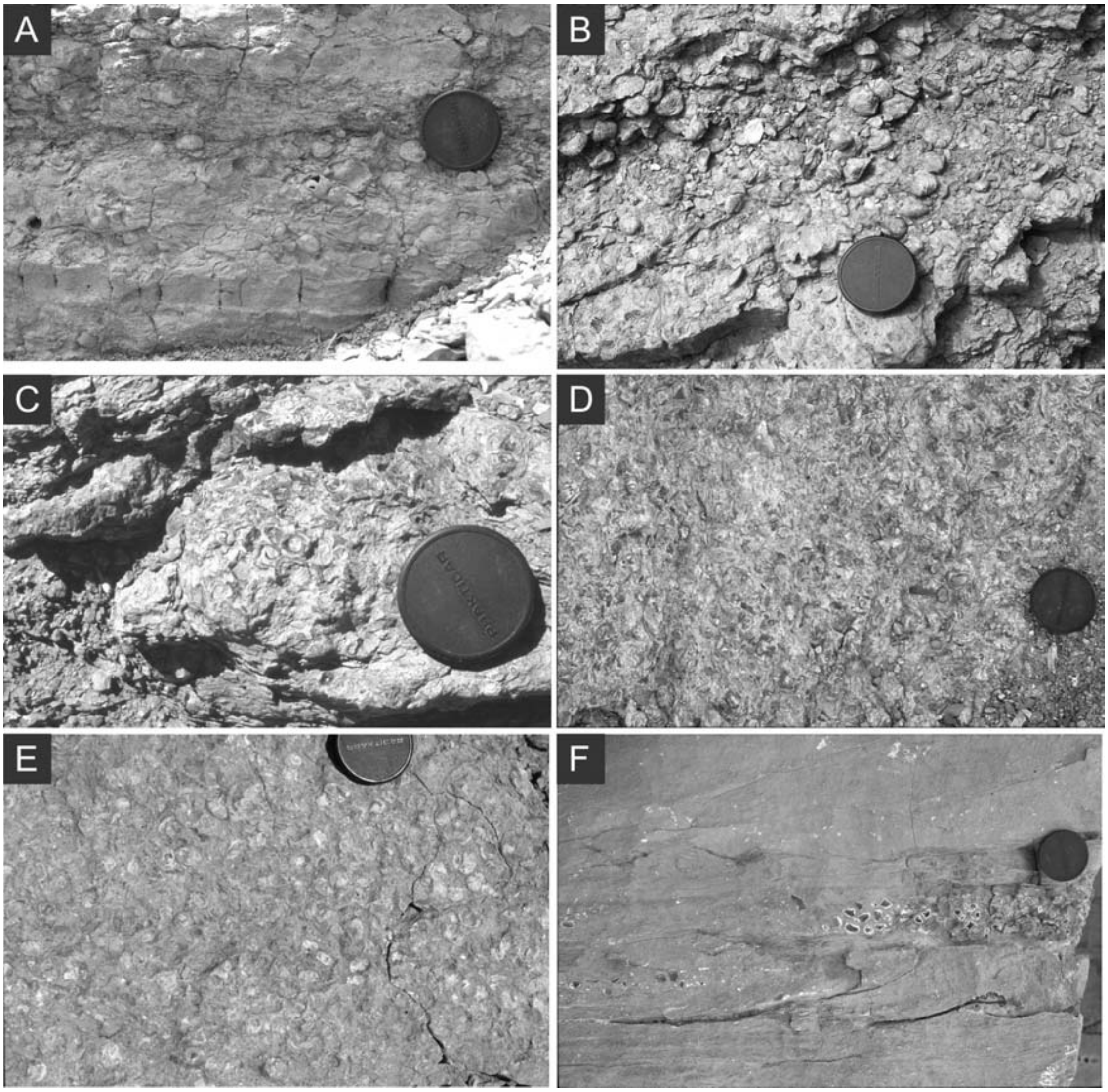


Figure 10 - A. Cross-section through a brachiopod shell bed that consists of small scale alternation of moderately sorted floatstones containing clusters of articulated shells and well sorted packstones/rudstones. B. Bedding plane view of the same bed, showing clusters of the multicostate rhynchonellid *Rhactorhynchia*. C. Cross-section through a densely packed shell bed dominated by disarticulated valves of the cementing bivalve *Liostrea sandalina*. D. Bedding plane view of densely packed and moderately/poorly sorted marl with a highly diverse assemblage dominated by *Liostrea sandalina*. E. Bedding plane view of a pavement formed by disarticulated terebratulid brachiopods *(Stiphrothyris)*. F. Cross-section through a densely packed nest with brachiopods within a cross-bedded ooidal grainstone. It is dominated by the rhynchonellid *Rhactorhynchia*. Lens cap for scale.

Methods

The absolute abundance of brachiopod and bivalve individuals was estimated with the maximum number of individuals (XNI) approach. Brachiopods were determined by A.T. and bivalves by F.T.F. The samples used in the analyses contain more than 20 specimens. Untransformed relative abundances of brachiopods and bivalves from 118 samples were analyzed in exploratory and confirmatory multivariate analyses. All species were used in Q-mode analyses. Species that are represented by less than 5 specimens were removed in R-mode analyses based on species abundances. These include 29 species (*Sphaeroidothyris* sp., *Isognomon* sp., *Bositra* sp., *Plagiostoma* sp. D, *Ctenostreon* sp., *Oxytoma* sp., *Tancredia* sp., ?*Coeloastarte*, ?*Pressastarte* sp., Heterodont A, Heterodont B, *Opis (Trigonopis)* sp., *Pholadomya (Pholadomya)* sp., *Nuculoma* sp., ?*Ceratomyopsis* sp., ?*Eocallista* sp., *Thracia* sp., *Prorokia* sp., ?Inoceramid sp., ?*Rollieria* sp., *Eopecten* sp., ?*Plectomya* sp., *Limatula* sp., *Trichites* sp., *Nuculana* sp., *Unicardium* sp., *Osteomya* sp., *Cercomya (Capillimya)* sp. and *Indocorbula* sp.). R-mode based analyses of similarities (ANOSIM) evaluated whether abundance patterns differ (1) among brachiopods and bivalve species, (2) among nine guilds, and (3) among five groups differing in the gill type.

Differences in community composition among environmental factors were evaluated with respect to differences (1) among habitats with distinct wave-base level/water depths (i.e., habitats above FWWB, above NSWB, below NSWB, and below MSWB), (2) among habitats differing in the rate of siliciclastic and carbonate input (i.e., limestones, marly limestones, and marls), and (3) among habitats differing in the substrate consistency (i.e., soft-bottom habitats with dispersed bioclasts and signs of bioturbation, mixed-bottom habitats with mud and common brachiopods, mollusks, serpulid and corals, and oolite and skeletal bars). Well sorted and densely packed, ooidal and bioclastic grainstones were assigned to habitats above FWWB (i.e., inner ramp). Amalgamated, well/moderately sorted bioclastic packstones and rudstones with interstitial micrite were assigned to habitats above NSWB (i.e., mid-ramp). Moderately/poorly sorted and densely/loosely packed deposits with internal stratification (i.e., multiple-event beds) consisting of small-scale alternation of mudstones, floatstones and packstones were assigned to habitats above MSWB (i.e., outer ramp). 1 cm-thick layers or pavements with concentrations of bioclasts within the siliciclastic intervals were also assigned to habitats above MSWB. Mudstones, wackestones and floatstones with missing signs of episodic, high-energy disturbance were assigned to habitats below MSWB (i.e., basin). Deposits with in situ corals or with biologically-degraded corals showing no signs of physical damage were also assigned to this habitat type.

Q-mode based ANOSIM evaluating differences in community composition were used in three steps. First, one-way analyses tested whether there are any differences among habitats differing in the siliciclastic supply, wave-base level and substrate consistency. This approach does not take into accout any possible interactions among the three factors. Second, two-way analyses tested whether there are any differences among habitats differing in one environmental factor (e.g., siliciclastic supply), keeping variation in another factor (e.g., wave-base level) constant. Third, two-way analyses evaluating effects of two factors (e.g., siliciclastic supply and wave-base level) were restricted within one group of the third factor (e.g., soft substrate). This approach enables to assess whether effects of one environmental factor have significant effects on community composition so that other two factors are kept constant.

To evaluate relationship between shell density and bed thickness, all beds were assigned to three qualitative ranks: (1) beds with rare or dispersed shells, (2) beds with loosely packed shells, and (3) beds with densely packed shells. It was evaluated whether thicker beds are characterized by a lower shell density. This prediction follows from the null scenario under which shell density is minimized by sediment dilution (Kidwell, 1985). This relationship was evaluated in three areas: (1) the southwestern part of the CHARB represented by the Tidrit section, (2) the eastern part of the basin represented by the Bou Kendill and Assameur sections, and (3) the northeastern margin of the basin represented by the Talghemt and Kasba Flilo sections. Only beds thicker than 5 cm were analyzed. Beds with in situ corals and coral debris and high-energy oolite and skeletal bars were excluded, and the analysis was restricted to the Agoudim Formation and the middle member of the Bin El Ouidane Formation.

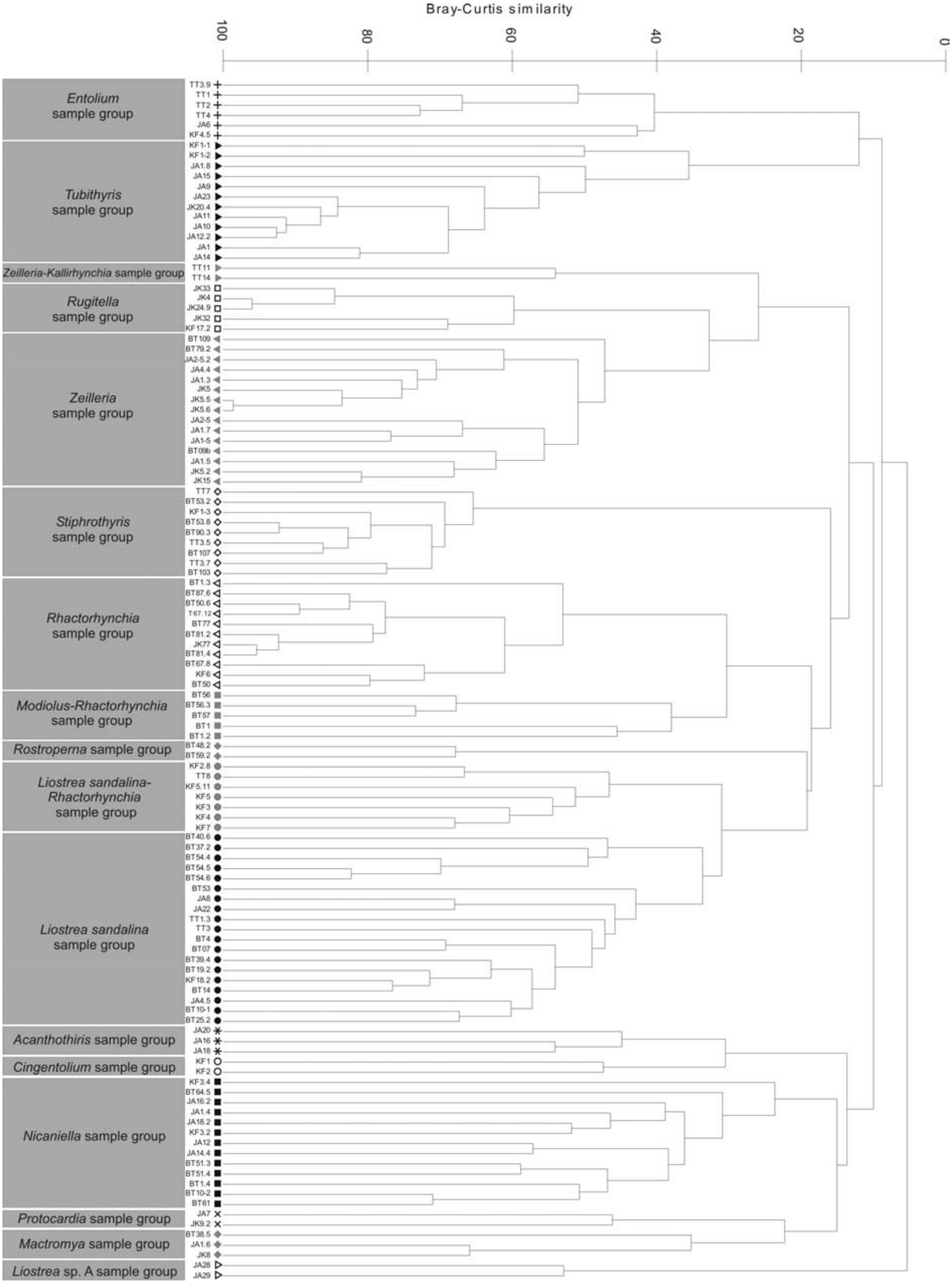


Figure 11 - 17 sample groups discriminated by Q-mode cluster analysis performed with the group-average linking method and Bray-Curtis similarity. The analysis was based on relative abundances of brachiopod and bivalve species.

Benthic communities

The Q-mode cluster analysis based on untransformed relative abundances and using group-average linking method discriminated 17 sample groups at a Bray-Curtis similarity of approximately 30-40 (Fig. 11). The analysis is based on 118 samples with 8041 individuals. Seven groups are dominated by pedunculate brachiopods, seven groups are dominated by bivalves, and three groups contain equally abundant brachiopods and bivalves (Figs. 12-13).

(1) The *Rugitella* sample group is represented by five samples with 318 specimens. Its sample-level richness ranges between 2 and 6 and the evenness (PIE) is relatively low to moderate (0.29-0.64). It is dominated by the pedunculate brachiopods *Rugitella prebullata* (72%) and *Zeilleria subbuculenta* (8%), and the cementing oyster *Liostrea sandalina* (13%). Free-lying filibranchs are less common (2%). Other guilds are rare or absent. This group occurs mainly in wackestones/floatstones and coral debris floatstones in the upper member. They correspond mainly to habitats above MSWB and above NSWB.

(2) The *Zeilleria* sample group is defined on the basis of 15 samples with 759 individuals. The sample-level richness is between 2 and 12. The evenness (PIE) is rarely low (0.27) and mostly moderately high (0.51-0.76). It is comparable to the *Rugitella* sample group, with the reversed rank abundance of the two zeillerioid brachiopods. The pedunculate brachiopods *Zeilleria subbucculenta* (50%) and *Rugitella prebullata* (18%), and the cementing oyster *Liostrea sandalina* (15%) are abundant. Epibyssate filibranchs (3%) and shallow burrowing eulamellibranchs (2.9%) are less common and other guilds are rare (< 2%). This group occurs mainly in the carbonate intervals and less commonly in the siliciclastic intervals of the middle member that correspond to habitats below MSWB. In the carbonate intervals, this group occurs in coral debris and serpulid (*Filograna*) floatstones. Several samples come from ooidal packstones and grainstones of the upper member that reveal habitats above NSWB and above FWWB.

(3) The *Zeilleria-Kallirhynchia* sample group consists of two samples with 94 individuals that occur in coral debris floatstones and bioclastic packstones of the upper member. These deposits correspond to habitats above NSWB. The sample-level richness is between 7 and 9 and the evenness is relatively high (0.72-0.86). It is dominated by the pedunculate brachiopods (68%) and epibyssate filibranchs (23%). The brachiopods are represented by the smooth zeillerioid *Zeilleria subbucculenta* (27%), the multicostate rhynchonellid *Kallirhynchia* aff. *oranensis* (27%), and the terebratuloid *Stiphrothyris mouterdei* (14%). The epibyssate bivalves are mainly represented by *Chlamys* sp. (11%) and *Plagiostoma* sp. C (10%). Cementing pseudolamellibranchs (5.1%) and free-lying filibranchs (3.4%) are less common. Infaunal guilds are absent.

(4) The *Rhactorhynchia* sample group is represented by 11 samples with 1330 individuals. Its sample-level richness varies between 2 and 10. The evenness (PIE) is highly variable (0.08-0.71). It is dominated by the multicostate rhynchonellid *Rhactorhynchia* sp. A (72%). Other brachiopods as *Zeilleria subbucculenta* (2%) and *Stiphrothyris mouterdei* (1%) are rare. Cementing pseudolamellibranchs, represented mainly by *Liostrea sandalina* (10%), are abundant. Epibyssate (*Bakevellia* sp., *Rostroperna* sp.) and endobyssate filibranchs (*Modiolus* sp.) are less common. Other bivalve guilds are rare (< 2%). This group occurs in ooidal packstones and grainstones in the lower and upper members (habitats above FWWB), and in floatstones and shelly packstones in the carbonate intervals of the middle member (habitats above MSWB and NSWB).

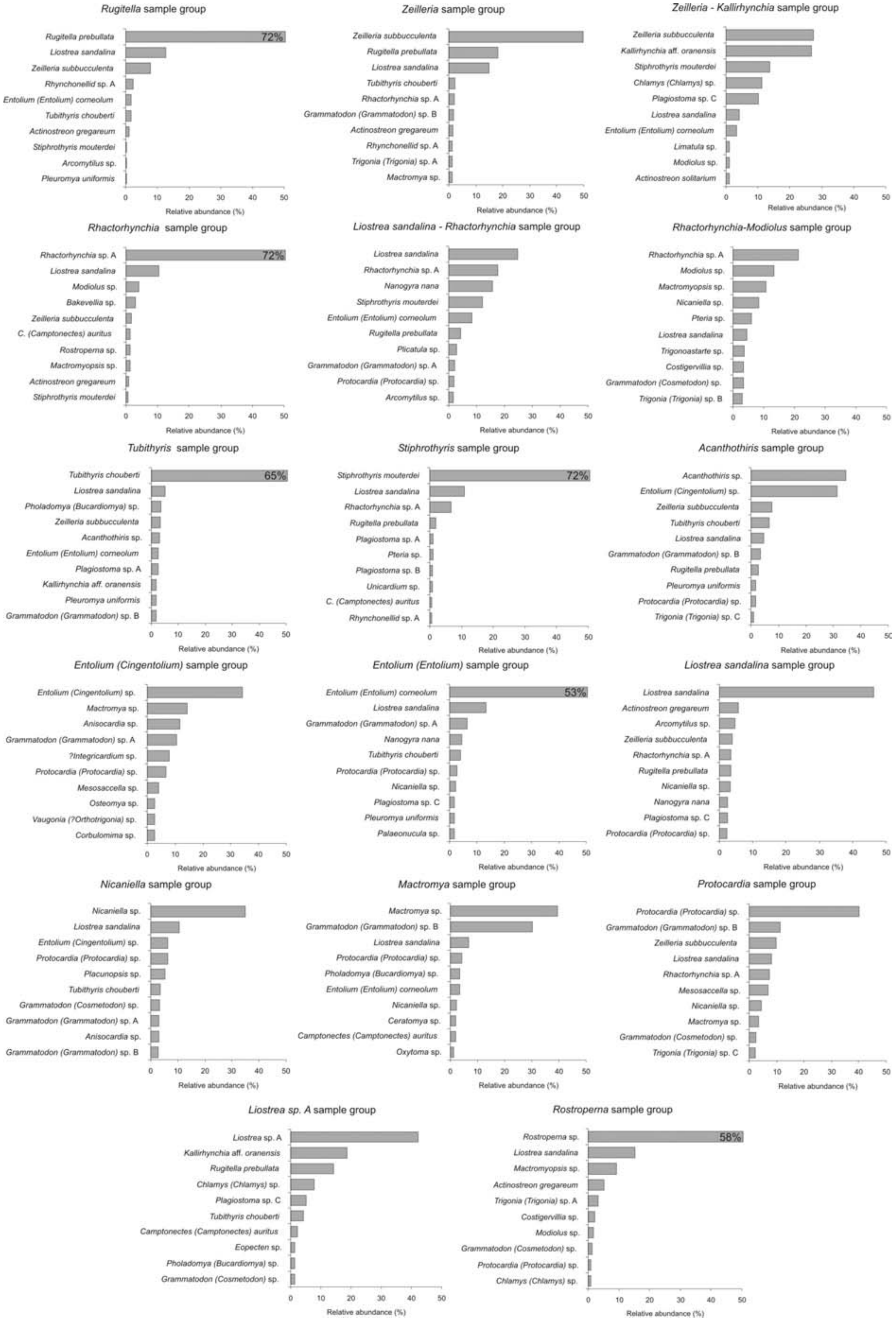


Figure 12 - Relative abundances of ten most common brachiopod and bivalve species in 17 sample groups.

(5) The *Liostrea sandalina – Rhactorhynchia* sample group consists of seven samples with 557 individuals. Its sample-level richness is between 7 and 13, the evenness is invariably high (0.76-0.84). The group is dominated by cementing pseudolamellibranchs *Liostrea sandalina* (25%) and *Nanogyra nana* (16%), and pedunculate brachiopods *Rhactorhynchia* sp. A (18%) and *Stiphrothyris mouterdei* (12%). Free-lying filibranchs are represented by *Entolium (Entolium) corneolum* (8%). Epibyssate filibranchs (5%), cementing filibranchs (3%), and shallow (2.5%) and deep burrowing eulamellibranchs (2.5%) are less common. Other guilds are rare (< 1%). This sample group invariably occurs in bioclastic and serpulid floatstones in the carbonate intervals of the middle member. They correspond to habitats above MSWB and above NSWB.

(6) The *Rhactorhynchia-Modiolus* sample group is represented by five samples with 635 individuals. The sample-level richness ranges between 10 and 23, the evenness (PIE) is very high (0.78-0.91). In terms of species abundances, the group is dominated by the multicostate rhynchonellid *Rhactorhynchia* sp. A (21%), endobyssate filibranch *Modiolus* sp. (13%), shallow burrowing eulamellibranchs *Mactromyopsis* sp. (11%) and *Nicaniella* sp. (8%), and epibyssate filibranch *Pteria* sp. (6%). Other bivalves as *Liostrea sandalina, Trigonastarte* sp., *Costigervillia* sp., *Grammatodon (Cosmetodon)* sp., *Trigonia (Trigonia)* sp. B and *Placunospis* sp. are also common (> 3%). In terms of guild abundances, the group is dominated by shallow burrowing eulamellibranchs (28%), pedunculate brachiopods (23%), and epibyssate (18%) and endobyssate filibranchs (17%). Cementing pseudolamellibranchs (5%) and filibranchs (3%), and shallow burrowing filibranchs (3%) and protobranchs (2%) are less common. This group is invariably bounded to coquinal marls (siliciclastic intervals) and coquinal marly limestones (carbonate intervals) of the lower and middle members. They correspond to habitats above MSWB.

(7) The *Tubithyris* sample group is defined on the basis of 12 samples with 652 individuals. With exception of one monospecific sample, its sample-level richness ranges between 4 and 11 species and the evenness (PIE) is highly variable (0.22-0.86). The smooth, highly biconvex and morphologically variable terebratuloid *Tubithyris chouberti* is most abundant (65%), with other pedunculate brachiopods *Zeilleria subbucculenta* (3%) and *Acanthothiris* sp. (3%) being less common. Cementing pseudolamellibranchs are represented by *Liostrea sandalina* (5%) and *Nanogyra nana* (1%), and epibyssate filibranchs mainly by genus *Plagiostoma* (4%). Deep burrowing eulamellibranchs are also common, represented by large-sized *Pholadomya (Bucardiomya)* sp. (3%) and *Pleuromya uniformis* (2%). Free-lying filibranchs are mainly represented by *Entolium (Entolium) corneolum* (3%), and shallow burrowing eulamellibranchs by *Nicaniella* sp. (2%). This group predominantly occurs in micrite-rich wackestones and floatstones in the siliciclastic and carbonate intervals of the middle member. These deposits correspond mainly to habitats below MSWB.

(8) The *Stiphrothyris* sample group is represented by nine samples with 557 individuals. Its sample-level richness is between 3 and 10 and the evenness (PIE) is low to moderate (0.24-0.64). The pedunculate brachiopods *Stiphrothyris mouterdei* (72%) and *Rhactorhynchia* sp. A (7%) are abundant. *Rugitella prebullata* (2%) is less common. Cementing pseudolamellibranchs (*Liostrea sandalina*) and epibyssate filibranchs (*Plagiostoma, Pteria, Camptonectes*) are also relatively abundant. Other bivalve guilds are rare (1%). This group is limited to the carbonate intervals of the middle and upper member. It is occurs in ooidal packstones, micrite-rich wackestones/floatstones, coral debris floatstones, and serpulid floatstones. These deposits correspond mainly to habitats above NSWB and above FWWB.

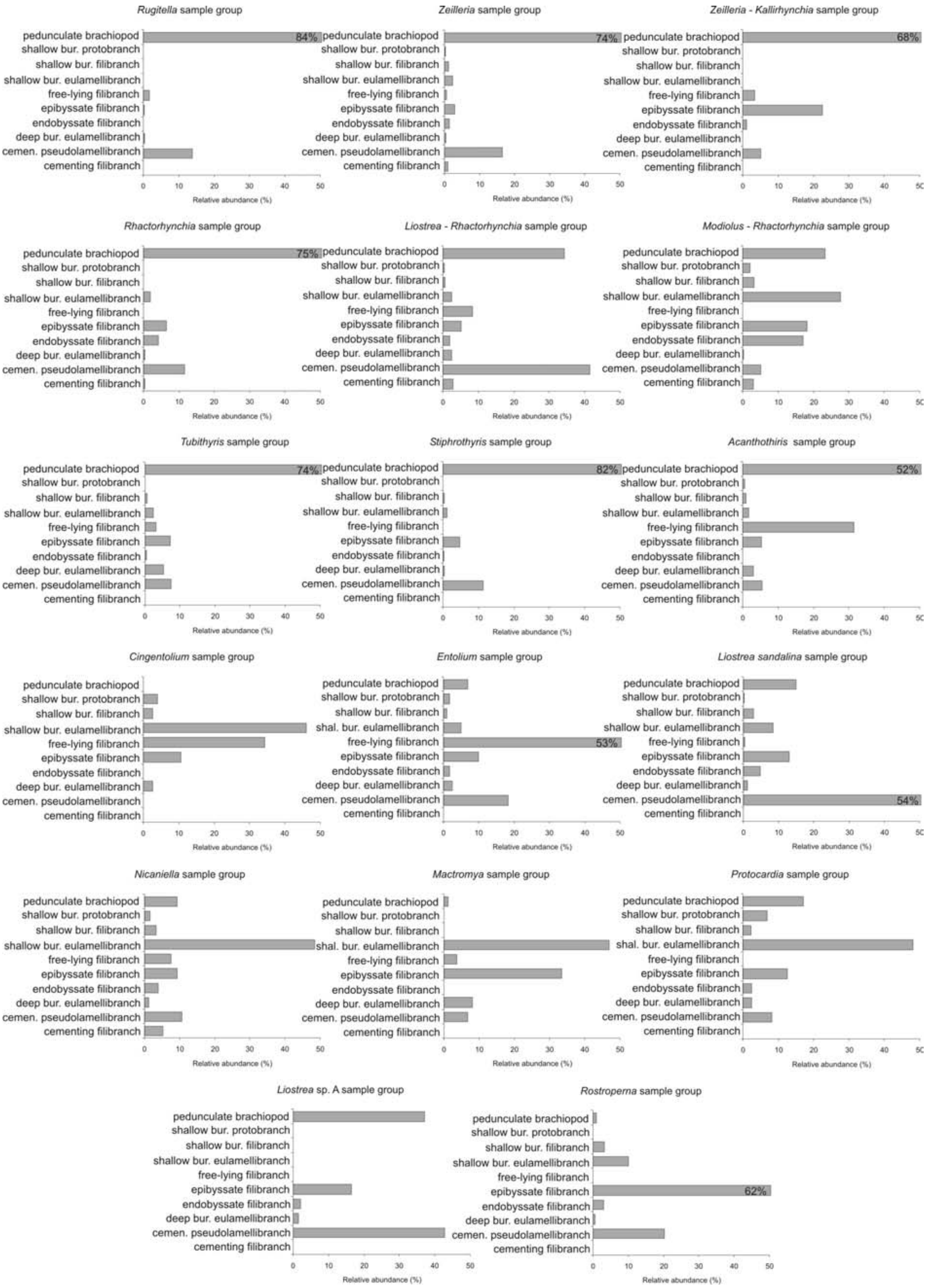


Figure 13 - Relative abundances of brachiopod and bivalve guilds in 17 sample groups.

(9) The *Acanthothiris* sample group is represented by three samples with 121 individuals. The sample-level richness varies between 3 and 12 and the evenness (PIE) is also variable (0.44-0.83). It is dominated by the pedunculate brachiopod *Acanthothiris* sp. (35%), followed by less common *Zeilleria subbuculenta* (8%), *Tubithyris chouberti* (7%), and *Rugitella prebullata* (3%). Bivalves are represented mainly by free-lying filibranchs (*Entolium (Cingentolium)* sp.) and cementing pseudolamellibranchs (*Liostrea sandalina*). Epibyssate filibranchs (*Grammatodon, Gervillaria, Camptonectes*) and deep burrowing eulamellibranchs (*Pleuromya, Pholadomya, Ceratomya*) are less common. This group is restricted to marly wackestones and floatstones of the carbonate intervals of the middle member. These deposits correspond to habitats below MSWB.

(10) The *Entolium (Cingentolium)* sample group consists of two samples with 76 individuals. The sample-level richness is 7 species and the evenness is relatively high (0.77-0.83). In terms of species abundances, the group is dominated by the free-lying filibranch *Entolium (Cingentolium)* sp. (34%), followed by shallow burrowing eulamellibranchs *Mactromya* sp. (14%), *Anisocardia* sp. (12%), ?*Integricardium* sp. (8%), and *Protocardia (Protocardia)* sp. (7%), and epibyssate filibrach *Grammatodon* (*Grammatodon*) sp. A (11%). In terms of guild abundances, shallow burrowing eulamellibranchs (46%) and free-lying filibranchs (34%) dominate, epibyssate filibranchs are less abundant (11%). Shallow burrowing protobranchs (4%), shallow burrowing filibranchs (3%), and deep burrowing eulamellibranchs (3%) are less common. This group is limited to marly mudstones and wackestones of the carbonate intervals of the middle member. They correspond to habitats below MSWB.

(11) The *Entolium* (*Entolium*) sample group is represented by six samples with 285 individuals. The sample-level richness ranges between 4 and 13 species and the evenness (PIE) is moderate to high (0.64-0.81). One sample is monospecific. The group is dominated by the free-lying filibranch *Entolium (Entolium) corneolum* (53%), followed by less common cementing pseudolamellibranchs *Liostrea sandalina* (13%) and *Nanogyra nana* (4%), and epibyssate filibranch *Grammatodon (Grammatodon)* sp. A (6%). Pedunculate brachiopods are represented mainly by *Tubithyris chouberti* (4%). Other brachiopod species are rare (1%). Shallow burrowing eulamellibranchs are mainly represented by *Protocardia (Protocardia)* sp. (3%) and *Nicaniella* sp (2%). This group is limited to marly, micrite-rich wackestones and floatstones, locally with serpulids. These deposits occur in the carbonate and siliciclastic intervals of the middle member and correspond to habitats below and above MSWB.

(12) The *Liostrea sandalina* sample group is defined on the basis of 19 samples with 1265 individuals. Its sample-level richness ranges between 3 and 21 species. The evenness (PIE) is low in one sample (0.32) but mostly moderate to high (0.45-0.89) in other samples. It is dominated by cementing pseudolamellibranchs *Liostrea sandalina* (46%) and *Actinostreon gregareum* (6%). Pedunculate brachiopods (15%), epibyssate filibranchs (13%), shallow burrowing eulamellibranchs (8%) and endobyssate filibranchs (*Modiolus* sp., *Pinna* sp.) are common. Pedunculate brachiopods are represented by equally abundant *Zeilleria subbucculenta* (3.7%), *Rhactorhynchia* sp. A (3.5%), and *Rugitella prebullata* (3.5%). Epibyssate filibranchs are represented mainly by *Arcomytilus* sp. (5%) and *Plagiostoma* sp. C (2%). Shallow burrowing eulamellibranchs are represented mainly by *Nicaniella* sp. (3%), *Protocardia (Protocardia)* sp. (2%), and *Mactromya* sp. (2%). Shallow burrowing filibranchs are less common (2%). Other bivalve guilds are rare (1%). This group is limited marly limestones and limestones of the siliciclastic and carbonate intervals of the lower and middle

members. It occurs in variable deposit types, including mudstones, wackestones/floatstones, coral debris floatstones, serpulid floatstones and coquinal packstones. They correspond mainly to habitats above MSWB and above NSWB.

(13) The *Nicaniella* sample group is represented by 13 samples with 999 individuals. Its sample-level richness varies between 4 and 13. The evenness (PIE) is moderate to high (0.62-0.87). One sample has very low evenness (0.17). This group is dominated by small shallow burrowing eulamellibranchs (48%), represented by *Nicaniella* sp. (35%), *Protocardia (Protocardia)* sp. (6%) and *Anisocardia* sp. (3%). Cementing pseudolamellibranchs (*Liostrea sandalina*), epibyssate filibranchs [*Grammatodon (Grammatodon), G. (Cosmetodon)*] pedunculate brachiopods (*Tubithyris chouberti, Ractorhynchia* sp. A., *Acanthothiris* sp.), and free-lying filibranchs (*Entolium (Cingentolium)* sp.) are common. In rank abundance, they are followed by cementing (5%), endobyssate (4%), and shallow burowing filibranchs (3%). Deep burrowing bivalves and deposit-feeders are rare. This group occurs in marls and marly mudstones and wackestones of the siliciclastic intervals of the lower and middle members. These deposits correspond to habitats below and above MSWB.

(14) The *Mactromya* sample group consists of three samples with 88 individuals. The sample-level richness is between 6 and 7 and the evenness (PIE) is moderate to high (0.59-0.74). It is dominated by the shallow burrowing eulamellibranch *Mactromya* sp. (39%) and epibyssate filibranch *Grammatodon (Grammatodon)* sp. B (30%). The cementing pseudolamellibranch *Liostrea sandalina* (7%), shallow burrowing eulamellibranchs *Protocardia (Protocadia)* sp. (4%) and *Nicaniella* sp. (2%), deep burrowing eulamellibranchs *Pholadomya (Bucardiomya)* sp. (4%) and *Ceratomya* sp. (2%), and free-lying filibranch *Entolium (Entolium) corneolum* (4%) are less common. Pedunculate brachiopods are rare (1%) and other bivalve guilds are absent. This group is limited to marls of the siliciclastic intervals of the middle member. They correspond to habitats below MSWB.

(15) The *Protocardia* sample group is represented by two samples and 63 individuals. Its sample-level richness varies between 7 and 9 and the evenness (PIE) is relatively high (0.76-0.83). In addition to the most abundant Protocardia (Protocardia) sp. (40%), shallow burrowing eulamellibranchs are mainly represented by *Nicaniella* sp. and *Mactromya* sp. Pedunculate brachiopods (*Zeilleria subbucculenta*, *Rhactorhynchia* sp. A), epibyssate filibranchs (*Grammatodon (Grammatodon)* sp. B), cementing pseudolamellibranchs (*Liostrea sandalina*), and shallow burrowing protobranchs (*Mesosaccella* sp.) are common. Endobyssate filibranchs, shallow burrowing filibranchs and deep burrowing eulamellibranchs are rare (2%). This group occurs in marls and marly limestones of the siliciclastic intervals of the middle member. These deposits correspond to habitats below MSWB.

(16) The *Liostrea* sp. A sample group is represented by two samples with 105 specimens. Its sample-level richness ranges between 6 and 11. The evenness (PIE) is moderate to high (0.58-0.84). The group is dominated by the cementing pseudolamellibranch *Liostrea* sp. A (42%), followed by the pedunculate brachiopods *Kallirhynchia* aff. *oranensis* (19%) and *Rugitella prebullata* (14%). Epibyssate filibranchs *Chlamys (Chlamys)* sp. (8%) and *Plagiostoma* sp. C (5%) are common. Endobyssate filibranchs (2%) and deep burrowing eulamellibranchs (1%) are less common and other bivalve guilds are absent. This group occurs in coral debris floatsones and coral framestones of the upper member. They correspond to habitats

(17) The *Rostroperna* sample group consists of two samples with 137 specimens. The sample-level richness is between 8 and 9 and the evenness (PIE) is moderate (0.58-0.65). The group is dominated by the thick-shelled epibyssate filibranch *Rostroperna* sp. (58%), followed by cementing

pseudolamellibranchs *Liostrea sandalina* (15%) and *Actinostreon gregareum* (5%), and shallow burrowing eulamellibranch *Mactromyopsis* sp. (9%). Endobyssate filibranchs (*Modiolus* sp., *Grammatodon (Cosmetodon)* sp.), and shallow burrowing filibranchs (*Trigonia (Trigonia)* sp. A) are less common. Pedunculate brachiopods are rare (< 1%). This group occurs in marly limestones of the siliciclastic and carbonate intervals of the middle member. They correspond to habitats above MSWB.

Compositional differences among brachiopod- and bivalve-dominated samples

In Q-mode NMDS based on species abundances (Fig. 14A), the sample groups dominated by brachiopods and bivalves show a substantial overlap. However, the plot shows a relatively high stress value (0.21), indicating that the two-dimensional restoration might not completely capture rank order relationships among the samples. The NMDS plot shows that there are no natural groupings among the samples that show a rather gradation in community composition. In general, the sample groups dominated by shallow burrowing and free-lying bivalves are less similar to brachiopod sample groups than the sample groups dominated by cementing and endobyssate bivalves. In Q-mode NMDS based on guild abundances (Fig. 14B), brachiopod and bivalve sample groups show a slight overlap, with the mixed sample groups in intermediate position.

Co-occurrence patterns of brachiopods and bivalves

R-mode NMDS based on abundances of species > 5% per sample indicates that there are very low and insignificant differences among brachiopod and bivalve abundance patterns (R = 0.08, p = 0.16, Tab. 1). Similarly, there are very low and insignificant differences in abundance patterns among five groups subdivided according to their gills (i.e., brachiopods with lophophores, protobranch, filibranch, pseudolamellibranchs and eulamellibranch bivalves), and among ten guilds (Tab. 1). Posterior pairwise comparisons examining differences between particular groups would not be statistically valid because the global tests are insignificant (Clarke and Warwick, 2001). However, relationship between brachiopods and eulamellibranch bivalves is specifically examined because of the prior ecological hypothesis about their distinct feeding and substrate strategies (Tomašových, 2006b). Indeed, brachiopods and eulamellibranch bivalves significantly differ in abundance patterns (R = 0.365, p = 0.0002). This difference is visualized in a partial segregation between these two groups in R-mode NMDS (Fig. 14C). This difference is enhanced when pedunculate brachiopods are compared with shallow burrowing eulamellibranchs only (0.497, p = 0.00015). In addition, pedunculate brachiopods also differ in abundance pattern from cementing filibranchs (R = 0.453, p = 0.044), and shallow burrowing protobranchs (R = 0.571, p = 0.044). When the R value is computed for soft-bottom and mixed-bottom habitats separately, the difference between brachiopods and eulamellibranch bivalves is lower although also significant (R [soft-bottom habitats] = 0.16, p = 0.036, R [mixed-bottom habitats] = 0.3, p = 0.013).

R-mode NMDS based on guild abundances (Fig. 14D) and Bray-Curtis similarities (BC) indicate that pedunculate brachiopods shared their abundance patterns mainly with cementing pseudolamellibranchs (BC = 39) and epibyssate filibranchs (BC = 31), and less commonly with deep burrowing eulamellibranchs (BC = 23) and endobyssate filibranchs (BC = 23). BC similarities between brachiopods and other guilds are below 15. In accord with the results of R-mode ANOSIM based on species abundances, shallow burrowing eulamellibranchs share more similarity with shallow burrowing protobranchs, shallow burrowing filibranchs, endobyssate filibranchs, and epibyssate filibranchs than with pedunculate brachiopods.

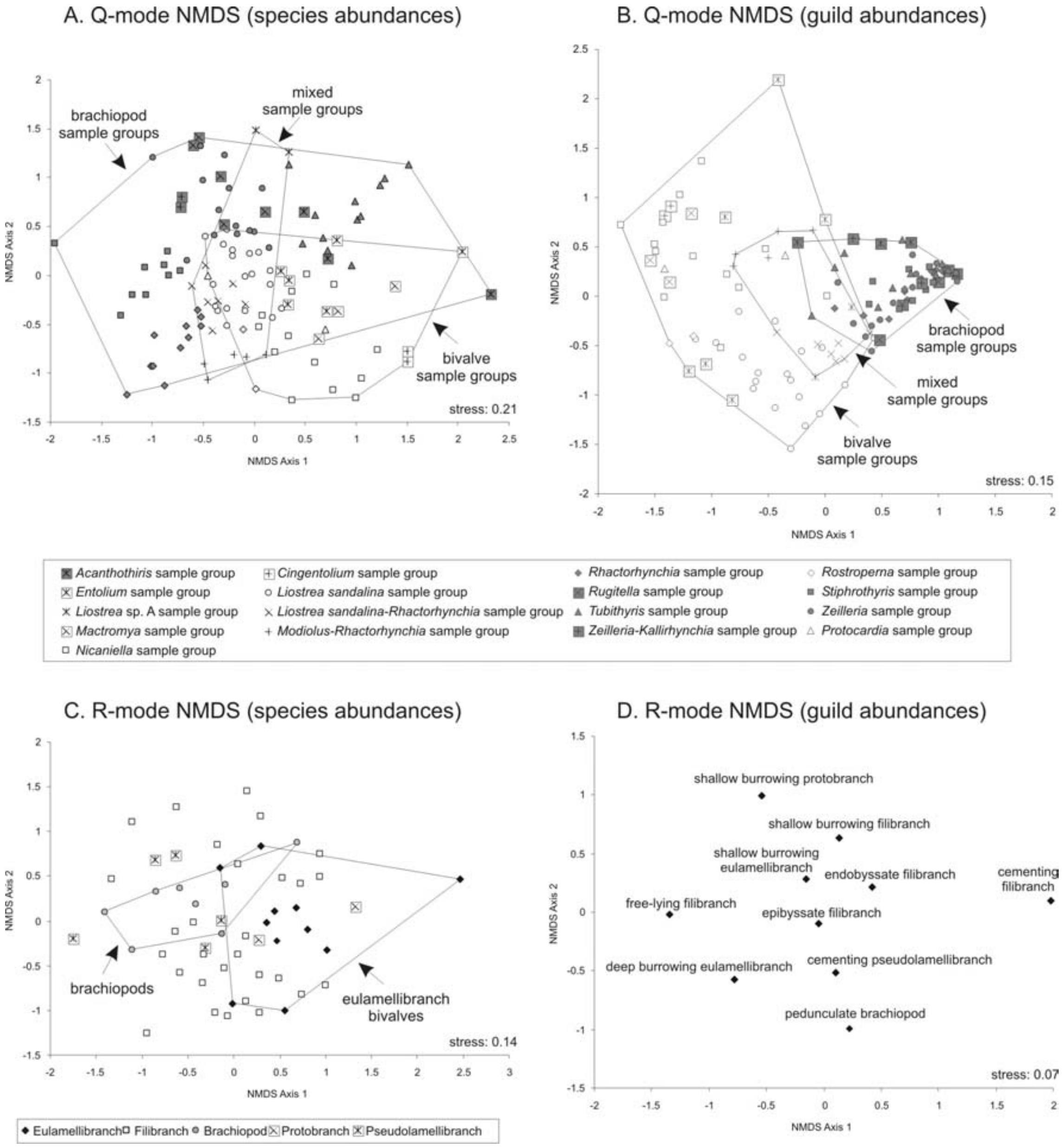


Figure 14 - Compositional relationship between samples and sample groups based on species and guild abundances. The compositional segregation among brachiopod, mixed, and bivalve sample groups is indicated by envelopes. A. Q-mode non-metric multidimensional scaling (NMDS) of 118 samples based on species abundances. B. Q-mode NMDS of 118 samples based on guild abundances. C. R-mode NMDS of brachiopod and bivalve species > 5% per sample based on taxonomic abundances. D. R-mode NMDS based on guild abundances.

Temporal effects

The differences in sample-level composition among three stratigraphic members are very low but significant in terms of species abundances (R = 0.129, p = 0.009). Based on pairwise comparisons, the difference is between the upper member on one hand, and the lower (R = 0.14, p = 0.016) and middle members (R = 0.23, p = <0.0001) on the other. Pedunculate brachiopods and cementing pseudolamellibranchs were abundant in all three stratigraphic members. Abundances of shallow burrowing eulamellibranchs were high in the lower and middle members only. In terms of guild abundances, the differences among three stratigraphic members are insignificant and negative (R = -0.03, p = 0.7). When siliciclastic supply is kept constant, the differences among stratigraphic members are significant for species abundances (two-way ANOSIM, R = 0.17, p = 0.0027) and insignificant for guild abundances (two-way ANOSIM, R = -0.009, p = 0.51). Importantly, the differences among stratigraphic members are significant also when habitats are kept constant (two-way ANOSIM, R = 0.52, p < 0.0001 for species abundances, R = 0.17, p = 0.013 for guild abundances). Note that using two-way analyses, the differences in species abundances are substantially higher when compared to one-way analyses, and the differences in guild abundances also changed from insignificant to significant values. When substrate is kept constant, the differences among stratigraphic members are insignificant both for species (R = 0.063, p = 0.2) and guild abundances (R = -0.029, p = 0.65).

R-mode based ANOSIM	R	p-value	Number of permutations	Number of permuted R≥observed R
Brachiopod vs. bivalve species (> 5%)	0.08	0.16	10000	1641
Differences among gill types				
Global test	0.003	0.45	10000	4525
Brachiopods vs. protobranchs	**0.571**	**0.044**	45	2
Brachiopods vs. filibranchs	0.021	0.38	10000	3809
Brachiopods vs. pseudolamellibranchs	-0.076	0.7	1287	905
Brachiopods vs. eulamellibranchs	**0.365**	**0.0002**	10000	2
Protobranchs vs. filibranchs	-0.093	0.7	465	324
Protobranchs vs. pseudolamellibranchs	0.118	0.29	21	6
Protobranchs vs. eulamellibranchs	0.043	0.4	78	31
Filibranchs vs. pseudolamellibranchs	-0.058	0.68	10000	6801
Filibranchs vs. eulamellibranchs	-0.061	0.8	10000	8033
Pseudolamellibranch vs. eulamellibranchs	**0.314**	**0.015**	4368	66
Differences among guilds				
Global test	0.08	0.091	10000	914
brachiopod vs. shallow burrowing protobranch	**0.571**	**0.044**	45	2
brachiopod vs. endobyssate filibranch	0.19	0.08	1287	103
brachiopod vs. cementing pseudolamellibranch	-0.076	0.7	1287	905
brachiopod vs. epibyssate filibranch	0.063	0.21	10000	2094
brachiopod vs. cementing filibranch	**0.453**	**0.044**	45	2
brachiopod vs. free-lying filibranch	0.067	0.42	45	19
brachiopod vs. deep burrowing eulamellibranch	0.109	0.25	165	42
brachiopod vs. shallow burrowing eulamellibranch	**0.497**	**0.00015**	6435	1
brachiopod vs. shallow burrowing filibranch	0.277	0.042	495	21

Table 1 - R-mode based analysis of similarities (ANOSIM) showing poor differences in abundance patterns between (1) brachiopod and bivalve species, (2) among guilds subdivided according to their gill type, and (3) among guilds (only comparison of brachiopods with other guilds is shown). However, the difference in abundance pattern between brachiopods and eulamellibranch bivalves is relatively high and significant. Applying the Bonferroni correction for the comparison among groups differing in the gill type would lower the alpha value to 0.005 (0.05/10). Applying this correction for the comparison among the guilds would lower the alpha value to 0.0011 (0.05/45).

Effects of siliciclastic supply

One-way analyses. Analyzing the whole dataset, the differences in sample-level composition among marls, marly limestones and limestones are significant although very low for species abundances (one-way ANOSIM, R = 0.07, p < 0.0074) and low for guild abundances (one-way ANOSIM, R = 0.26, p < 0.0001). However, the low differences are mainly caused by a high variation in sample-level composition of marly limestones (Tab. 2). The difference between end-member marls and limestones is substantially higher for species abundances (R = 0.3, p = 0.0001) and very high for guild abundances (R = 0.93, p < 0.0001). The compositional differences among marls, marly limestones and limestones in species and guild composition, evaluated separately for three stratigraphic members, are visualized in Q-mode NMDS plots in Figure 15. Pedunculate brachiopods (68%) and cementing pseudolamellibranchs (19%) dominated and the other guilds were substantially less common (< 5%) in limestones. Pedunculate brachiopods (32%) decreased in abundance, cementing pseudolamellibranchs (24%) were equally abundant, and epibyssate filibranchs (14%) and shallow burrowing eulamellibranchs (12%) increased in abundance in marly limestones. Shallow burrowing eulamellibranchs (55%) dominated and the other guilds were less common (< 10%) in marls.

Separation of wave-base level effects. Two-way crossed analysis evaluates whether there are any differences in sample-level composition among marls, marly limestones and limestones, allowing for habitat differences (Tab. 2). When habitat is kept constant, the differences among limestones, marly limestones and marls are relatively low but significant in terms of species (R = 0.11, p = 0.03) and guild abundances (R = 0.2, p < 0.0001). However, high and significant differences in sample-level composition are between end-member limestones and marls, both for species (R = 0.46, p < 0.0001) and guild abundances (R = 0.94, p < 0.0001). The pedunculate brachiopods were invariably dominant in carbonate-rich habitats (i.e., limestones), although species abundances substantially varied along wave-base level gradient (Figs. 16-17). *Stiphrothyris mouterdei* and *Rhactorhynchia* sp. A decreased in abundances and *Tubithyris chouberti* increased in abundance towards deeper habitats. *Rugitella prebullata* and *Zeilleria subbucculenta* were equally abundant along wave-base level gradient. *Liostrea sandalina* peaked in abundance at intermediate depths in carbonate-rich habitats. Abundances of the other bivalve guilds slightly increased with depth in carbonate-rich habitats. Although marly limestones were characterized by the high variation in community composition, *Liostrea sandalina* was one of the most common inhabitants of this deposit type. *Liostrea sandalina* decreased in abundance towards deeper habitats and pedunculate brachiopods were comparatively common along wave-base level gradient. Abundance of free-lying filibranchs and shallow burrowing eulamellibranchs increased towards deeper habitat and epibyssate filibranchs peaked at intermediate depths. Siliciclastic-rich habitats (i.e., marls) were consistently dominated by the shallow burrowing eulamellibranchs (*Nicaniella* sp.), followed by less common cementing psedolamellibranchs, pedunculate brachiopods, epibyssate filibranchs, and free-lying filibranchs. Cementing bivalves decreased in abundance with depth in siliciclastic-rich habitats. Because habitat types co-vary to some degree with substrate types, two-way crossed analyses were further restricted to one substrate type. In soft-bottom habitats, the difference between marls and limestones is high and significant for species (R = 0.62, p = 0.0001) and guild abundances (R = 0.91, p < 0.0001). The difference between marls and limestones was not evaluated *within* mixed-bottom habitats and *within* oolite bars because they are not represented by any marls.

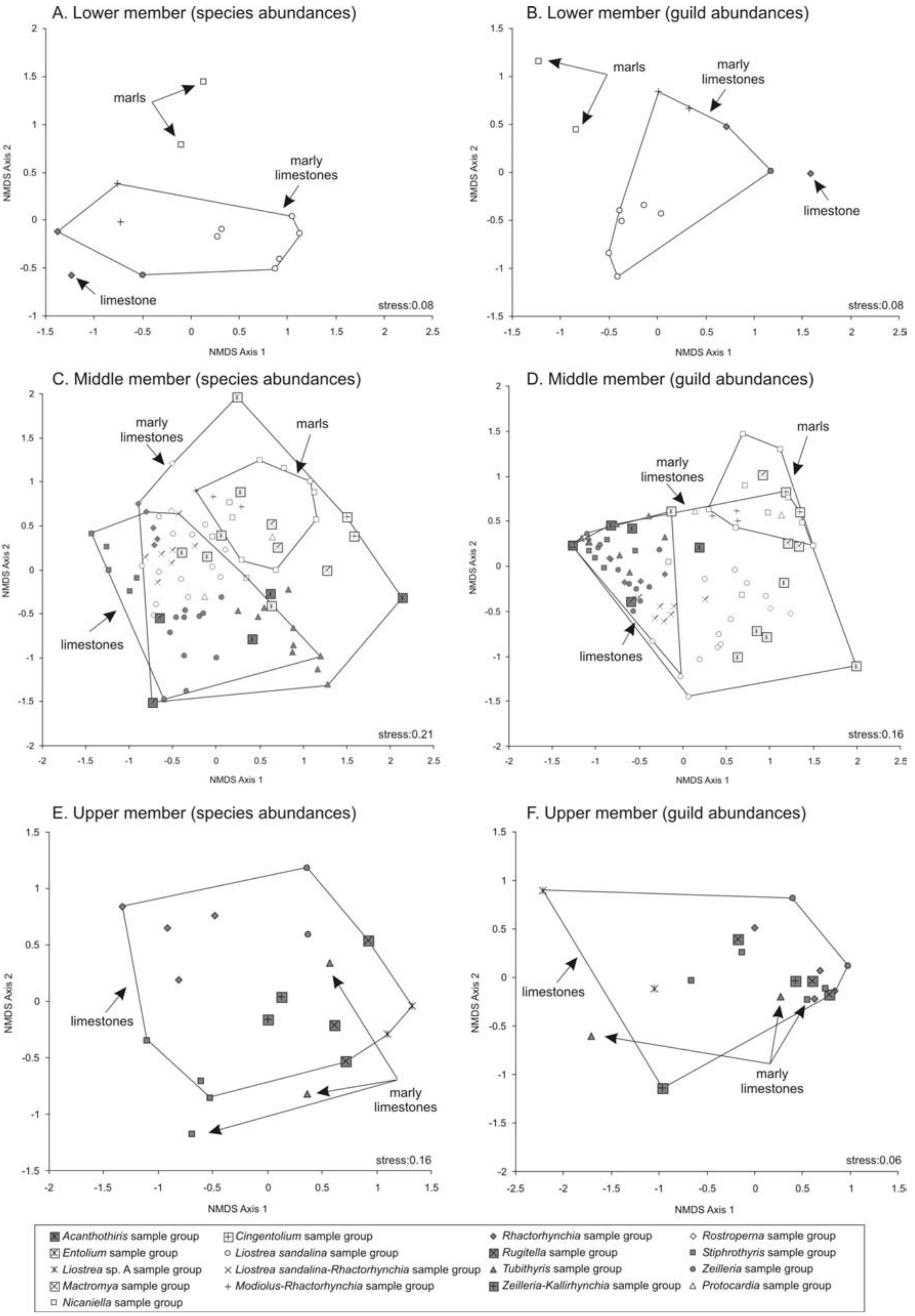


Figure 15 - Visualized differences in community composition among limestones, marly limestones and marls in three stratigraphic members based on species and guild abundances. A. Lower member - Q-mode NMDS based on species abundances. B. Lower member - Q-mode NMDS based on guild abundances. C. Middle member - Q-mode NMDS based on species abundances. D. Middle member - Q-mode NMDS based on guild abundances. E. Upper member - Q-mode NMDS based on species abundances. F. Upper member - Q-mode NMDS based on guild abundances.

One-way ANOSIM	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.074	0.0074	10000	74
limestone, marl	0.299	0.0001	10000	1
limestone, marly limestone	0.042	0.025	10000	246
marl, marly limestone	0.027	0.35	10000	3582
Guilds - global test	0.261	<0.0001	10000	0
limestone, marl	0.934	<0.0001	10000	0
limestone, marly limestone	0.149	0.0001	10000	1
marl, marly limestone	0.207	0.0028	10000	28

Two-way ANOSIM (siliciclastic effects, allowing for habitat effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.107	0.03	10000	296
limestone vs. marl	0.456	<0.0001	10000	0
limestone vs. marly limestone	0.092	0.057	10000	565
marl vs. marly limestone	0.001	0.457	10000	4568
Guilds - global test	0.201	<0.0001	10000	0
limestone vs. marl	0.942	<0.0001	10000	0
limestone vs. marly limestone	0.078	0.058	10000	583
marl vs. marly limestone	0.206	0.009	10000	90

Two-way ANOSIM (siliciclastic effects, allowing for substrate effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.026	0.24	10000	2379
limestone vs. marl	0.512	<0.0001	10000	0
limestone vs. marly limestone	-0.006	0.54	10000	5357
marl vs. marly limestone	-0.034	0.64	10000	6373
Guilds - global test	0.128	0.0003	10000	3
limestone vs. marl	0.919	<0.0001	10000	0
limestone vs. marly limestone	0.039	0.14	10000	1444
marl vs. marly limestone	0.073	0.15	10000	1475

Table 2 - Analyses of similarities (ANOSIM) testing effects of varying siliciclastic supply on species and guild composition. This is evaluated with (1) one-way analyses that do not take into account any possible interactions with wave-base level and substrate, (2) two-way crossed analyses that keep wave-base level constant, and (3) two-way crossed analyses that keep substrate consistency constant. Applying the Bonferroni correction for the pairwise comparisons lowers the alpha value to 0.017 (0.05/3).

Separation of substrate effects. Allowing for fact that there are substrate effects, two-way ANOSIM indicates that there are relatively high and significant differences in sample-level species composition between marls and limestones ($R = 0.51$, $p < 0.0001$, Tab. 2). Although the global test shows insignificant differences among three deposit types, this is related to the high compositional variation of marly limestones that completely overlap both with limestones and marls. In terms of guild abundances, the global test shows relatively low but significant differences among marls, marly limestones and limestones ($R = 0.13$, $p = 0.0003$). The difference between marls and limestones is strikingly high ($R = 0.92$, $p < 0.0001$). Note that abundance of brachiopods increased and abundance of shallow burrowing eulamellibranchs decreased with decreasing siliciclastic supply in soft-bottom habitats (Fig. 18). Two-way crossed analyses were further restricted to one habitat type. In habitats below MSWB, the difference between marls and limestones is high and significant for species (R =

0.61, p = 0.0006) and guild abundances (R = 0.9, p = 0.0002). Similarly, in habitats above MSWB, the difference between marls and limestones is high and significant for species (R = 0.68, p = 0.018) and guild abundances (R = 0.94, p = 0.018). In habitats above NSWB, the difference between marls and marly limestones is low for species (R = 0.17, p = 0.04) and guild abundances (R = 0.17, p = 0.05).

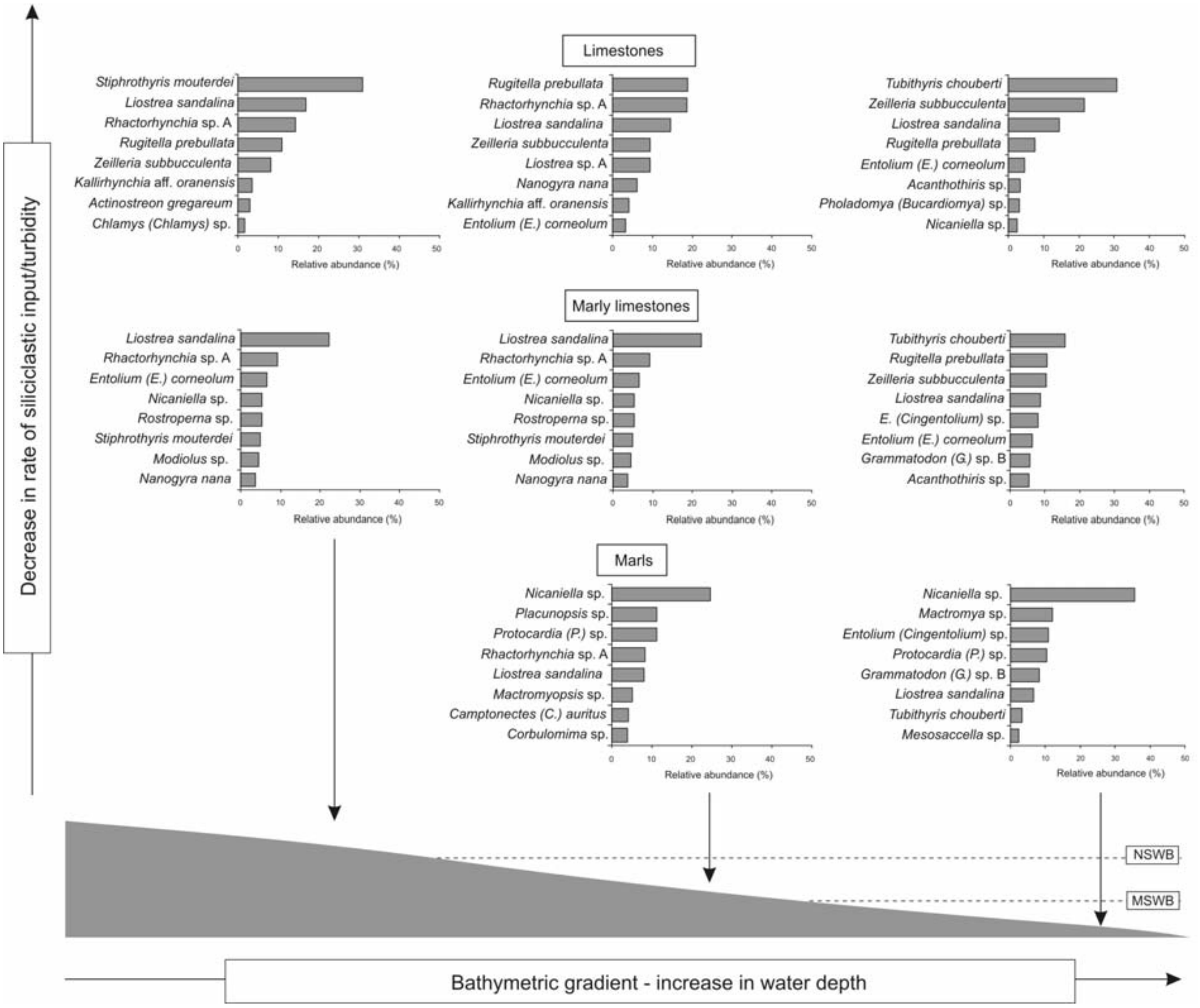


Figure 16 - Differences in species abundances among habitats with respect to varying wave-base level *and* siliciclastic supply.

Effects of wave-base level

One-way analyses. The differences in sample-level composition among four habitats in terms of wave-base level are low but significant for species abundances (R = 0.22, p < 0.0001), and very low for guild abundances (R = 0.08, p = 0.002). In terms of species abundances, pairwise comparisons show moderate and significant differences between habitats (R ranges between 0.23 and 0.47), with an exception of a very low difference between habitats above MSWB and above NSWB (R = 0.07, p = 0.054). In terms of guild abundances, pairwise comparisons show substantially lower between-habitat differences in comparison to those based on species abundances (Tab.). The pedunculate brachiopods *Tubithyris chouberti* (19%)*, Zeilleria subbucculenta* (13%), and *Rugitella prebullata* (8%), the cementing oyster *Liostrea sandalina* (10%), and the shallow burrowing eulamellibranch *Nicaniella* sp.

(8%) were common in habitats below MSWB. *Liostrea sandalina* (19%), the rhynchonellid brachiopod *Rhactorhynchia* sp. A (11%), and the shallow burrowing bivalve *Nicaniella* sp. (7%) were common in habitats above MSWB. *Liostrea sandalina* was also the most abundant species in habitats above NSWB (27%), followed by brachiopods *Stiphrothyris mouterdei* (20%) and *Rhactorhynchia* sp. A (15%). Habitats above FWWB were occupied mainly by the brachiopods *Rhactorhynchia* sp. A (54%), *Stiphrothyris mouterdei* (20%), and *Zeilleria subbucculenta* (14%).

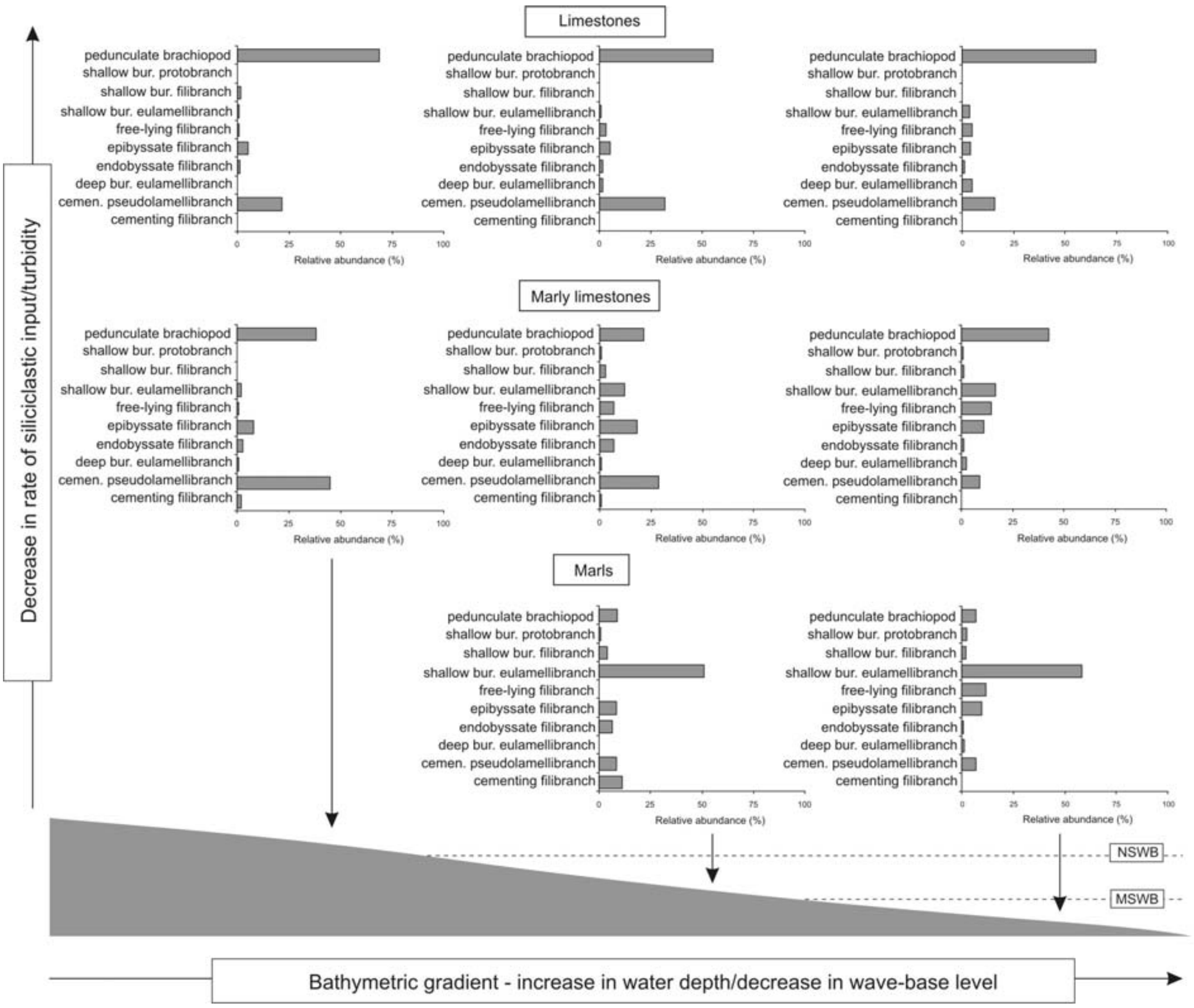


Figure 17 - Differences in guild abundances among habitats with respect to varying wave-base level *and* siliciclastic supply. Note that pedunculate brachiopods were invariably abundant in carbonate-rich habitats and shallow burrowing eulamellibranchs were consistently abundant in siliciclastic-rich habitats.

Separation of siliciclastic effects. Two-way crossed analysis evaluates whether there are any differences among depth habitats, allowing for differences in siliciclastic supply. When siliciclastic supply is kept constant, the differences among four habitats are significant but also relatively low in terms of species abundances (R = 0.247, p < 0.0001). The similar result follows for guild abundances, although the differences among habitats are lower (R = 0.12, p < 0.0001). As follows from pairwise comparisons based on species abundances, the deepest habitats below MSWB and the shallowest habitats above FWWB are well differentiated from habitats of intermediate depths (Tab. 3). To exclude any possible temporal effects and to keep siliciclastic supply relatively constant, the differences in species and guild composition among habitats were also evaluated within the middle member only and separately for limestone and marl intervals (Figs. 19-20). NMDS plots show that habitats consistently differ in species composition both in limestone and marl intervals, but between-habitat differences in guild composition are very poor. Because habitat types co-vary to some degree with substrate types, two-way crossed analyses were further restricted to one substrate type. Keeping the substrate constant, the differences among habitats are significant for species abundances only (R = 0.19, p = 0.002 for soft-bottoms, R = 0.19, p = 0.007 for mixed-bottoms). The differences among habitats are very low and insignificant for guild abundances (R = 0.05, p = 0.2 for soft-bottoms, R = 0.08, p = 0.1 for mixed-bottoms).

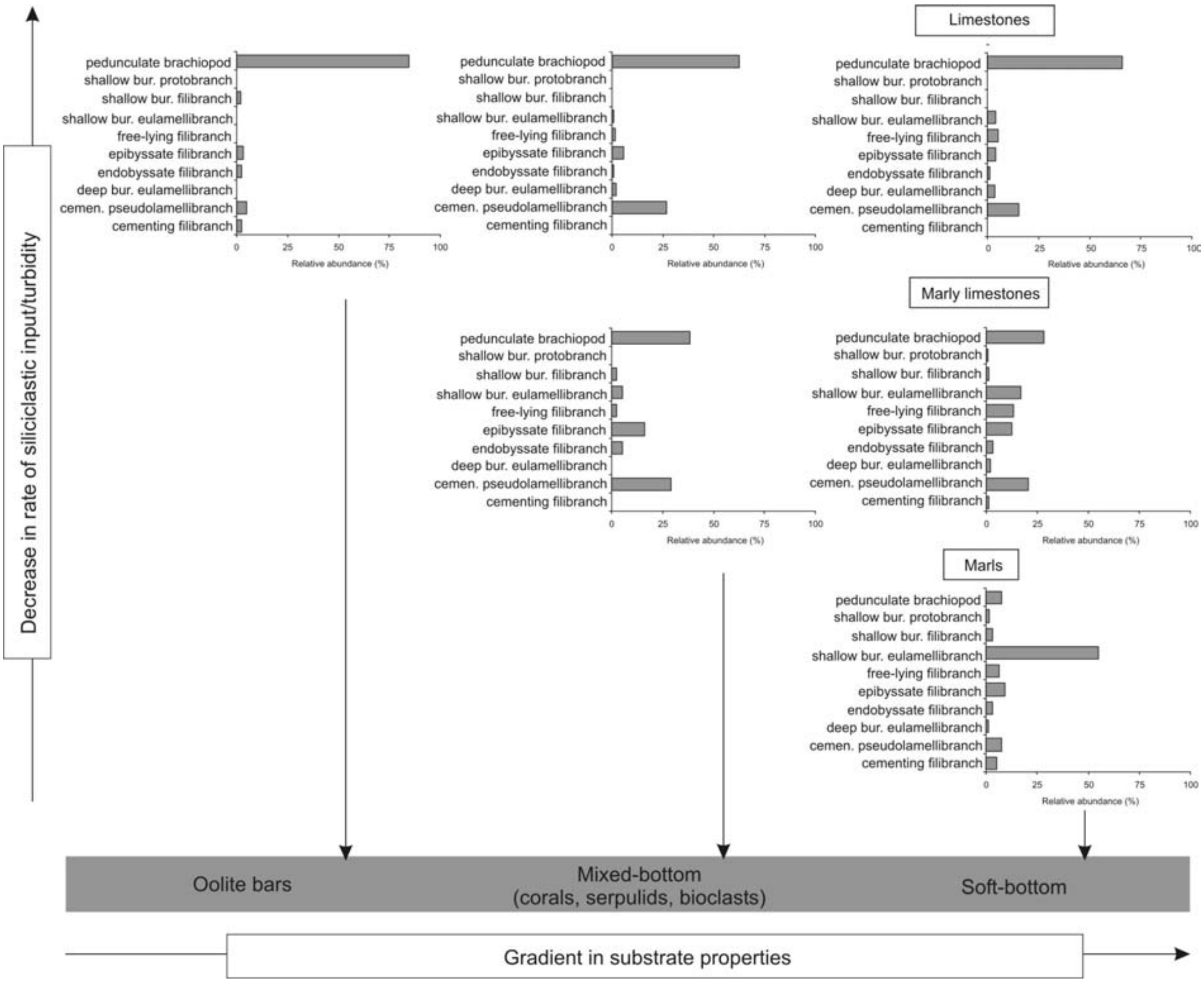


Figure 18 - Differences in guild abundances among habitats with respect to varying siliciclastic supply *and* substrate consistency. Note that brachiopods and shallow burrowing bivalves show differential preferences to varying siliciclastic supply in soft-bottom habitats.

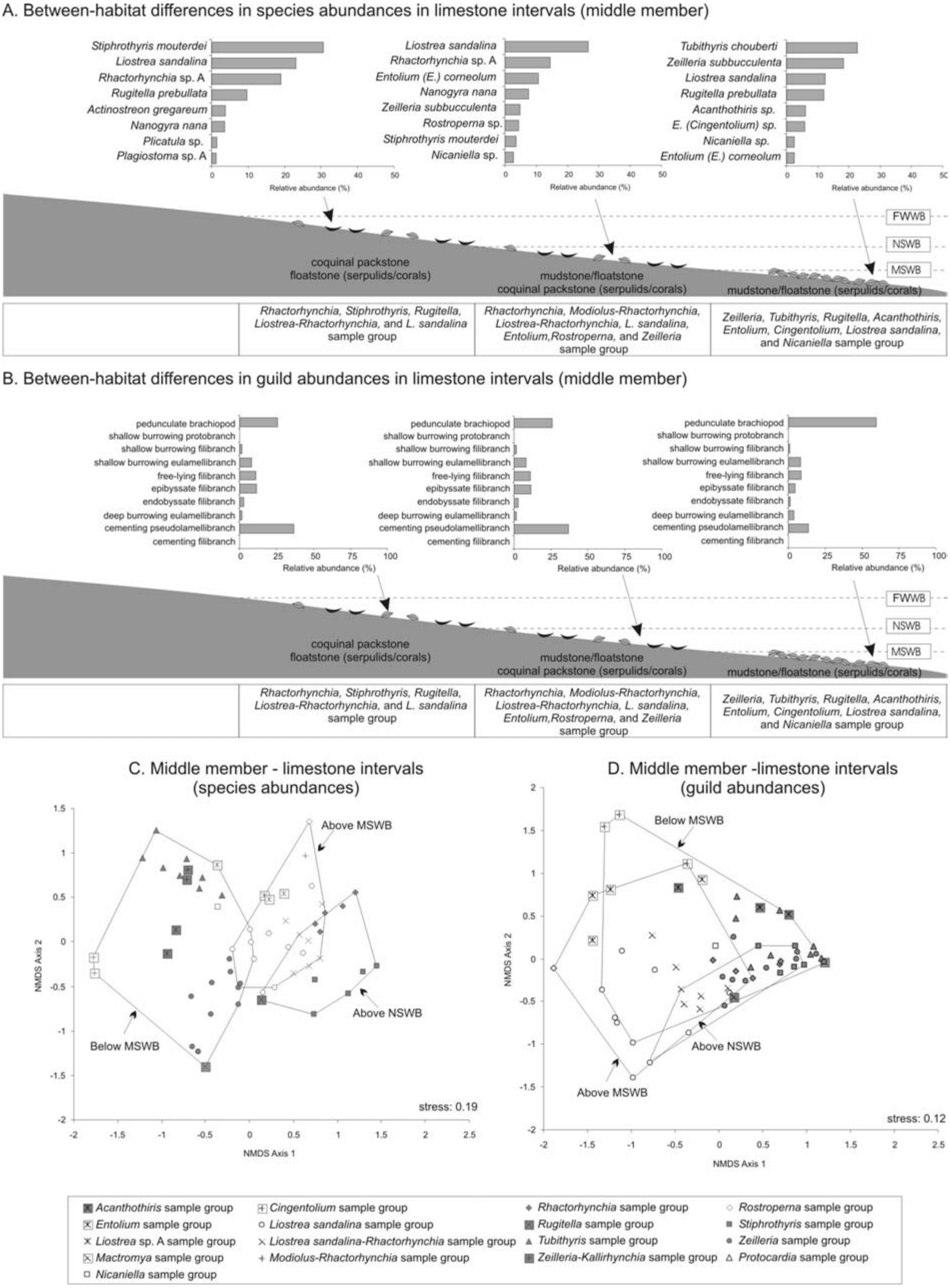
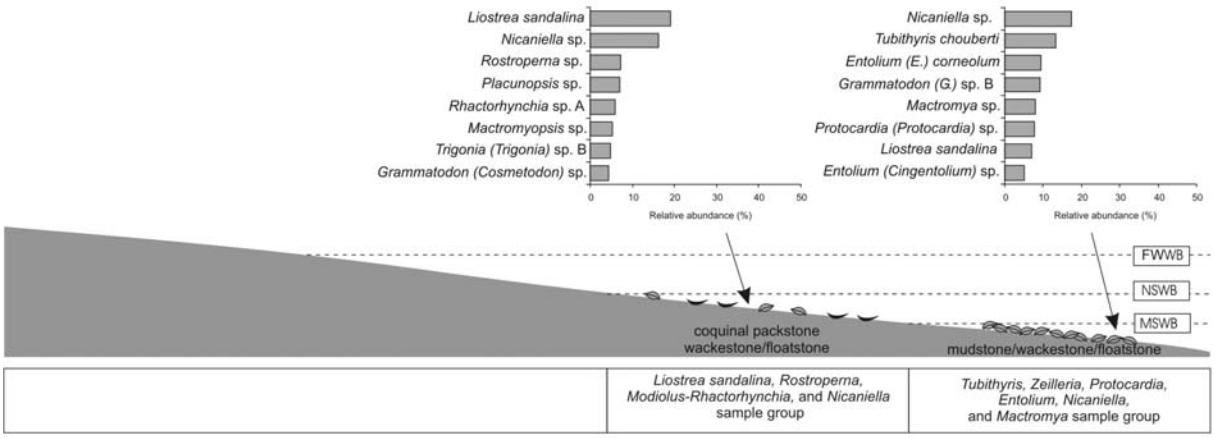
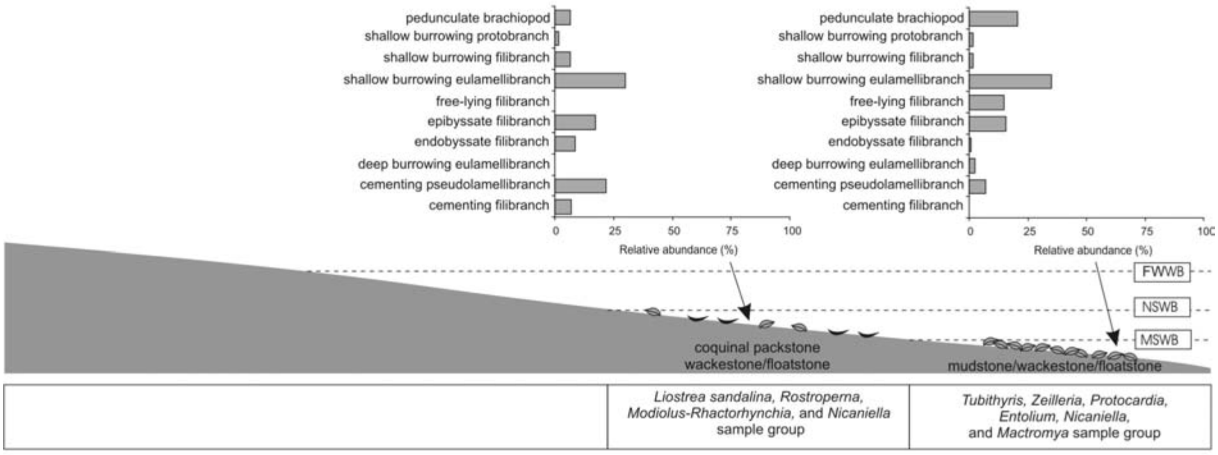


Figure 19 - Between-habitat differences in species (A) and guild abundances (B) *within* limestone intervals of the middle member Bin El Ouidane Formation and the Agoudim Formation. The compositional differences in species (C) and guild abundances (D) with respect to wave-base level are visualized in NMDS plots.

A. Between-habitat differences in species abundances in marl intervals (middle member)



B. Between-habitat differences in species abundances in marl intervals (middle member)



C. Middle member - marl intervals (species abundances)

D. Middle member - marl intervals (guild abundances)

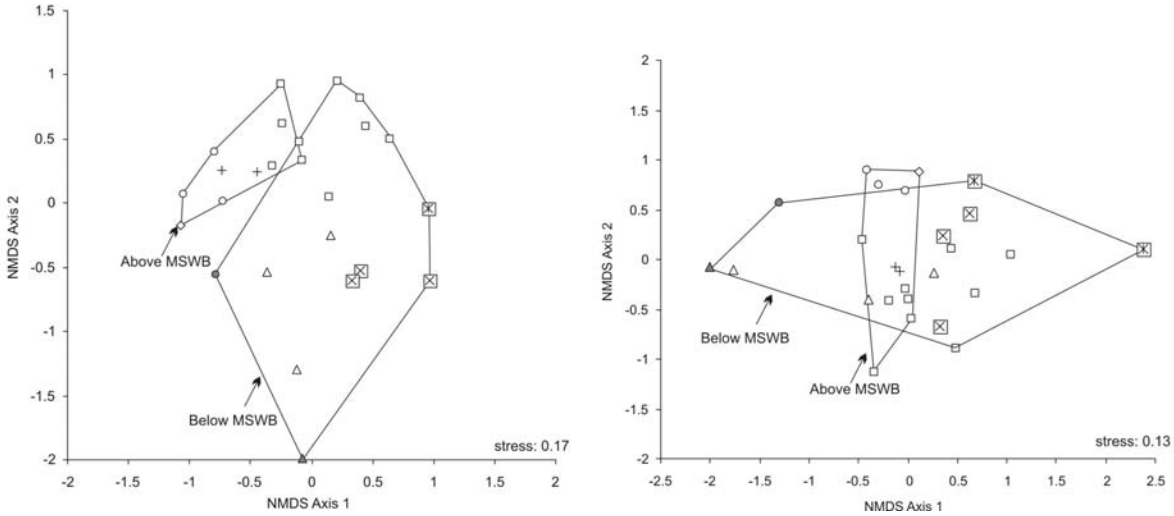


Figure 20 - Between-habitat differences in species (A) and guild abundances (B) *within* marl intervals of the middle member Bin El Ouidane Formation and the Agoudim Formation. The compositional differences in species (C) and guild abundances (D) with respect to wave-base level are visualized in NMDS plots. Both brachiopods and shallow burrowing bivalves increased and cementing bivalves decreased in abundance towards deeper habitats.

One-way ANOSIM	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.219	<0.0001	10000	0
below MSWB vs. above MSWB	0.229	<0.0001	10000	0
below MSWB vs. above FWWB	0.47	<0.0001	10000	0
below MSWB vs. above NSWB	0.235	<0.0001	10000	0
above MSWB vs. above FWWB	0.335	0.0045	10000	45
above MSWB vs. above NSWB	0.068	0.0542	10000	542
above FWWB vs. above NSWB	0.334	0.0009	10000	9
Guilds - global test	0.083	0.002	10000	18
below MSWB vs. above MSWB	0.128	0.0002	10000	2
below MSWB vs. above FWWB	-0.107	0.86	10000	8625
below MSWB vs. above NSWB	0.023	0.23	10000	2271
above MSWB vs. above FWWB	0.28	0.0015	10000	15
above MSWB vs. above NSWB	0.096	0.0128	10000	128
above FWWB vs. above NSWB	0.016	0.36	10000	3619

Two-way ANOSIM (habitat effects, allowing for siliciclastic effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.247	<0.0001	10000	0
below MSWB vs. above MSWB	0.323	<0.0001	10000	0
below MSWB vs. above FWWB	0.675	<0.0001	10000	0
below MSWB vs. above NSWB	0.23	0.0002	10000	2
above MSWB vs. above FWWB	0.184	0.039	10000	388
above MSWB vs. above NSWB	-0.019	0.57	10000	5752
above FWWB vs. above NSWB	0.314	0.0048	10000	48
Guilds - global test	0.118	0.0001	10000	1
below MSWB vs. above MSWB	0.176	0.0002	10000	2
below MSWB vs. above FWWB	0.029	0.32	10000	3229
below MSWB vs. above NSWB	0.052	0.12	10000	1208
above MSWB vs. above FWWB	0.358	0.0085	10000	85
above MSWB vs. above NSWB	0.002	0.47	10000	4712
above FWWB vs. above NSWB	0.006	0.4	10000	4051

Two-way ANOSIM (habitat effects, allowing for substrate effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.168	<0.0001	10000	0
below MSWB vs. above MSWB	0.182	<0.0001	10000	0
below MSWB vs. above FWWB	n.a.	n.a.	n.a.	n.a.
below MSWB vs. above NSWB	0.205	0.021	10000	206
above MSWB vs. above FWWB	n.a.	n.a.	n.a.	n.a.
above MSWB vs. above NSWB	0.141	0.024	10000	238
above FWWB vs. above NSWB	0.071	30.6	36	11
Guilds - global test	0.069	0.019	10000	190
below MSWB vs. above MSWB	0.1	0.0084	10000	84
below MSWB vs. above FWWB	n.a.	n.a.	n.a.	n.a.
below MSWB vs. above NSWB	-0.061	0.72	10000	7263
above MSWB vs. above FWWB	n.a.	n.a.	n.a.	n.a.
above MSWB vs. above NSWB	0.066	0.13	10000	1381
above FWWB vs. above NSWB	0.455	0.11	36	4

Table 3 - Analyses of similarities (ANOSIM) testing effects of varying wave-base level on species and guild composition. This is evaluated with (1) one-way analyses that do not take into account any possible interactions with siliciclastic supply and substrate, (2) two-way crossed analyses that keep siliciclastic supply constant, and (3) two-way crossed analyses that keep substrate consistency constant. Applying the Bonferroni correction for the pairwise comparisons lowers the alpha value to 0.0083 (0.05/6).

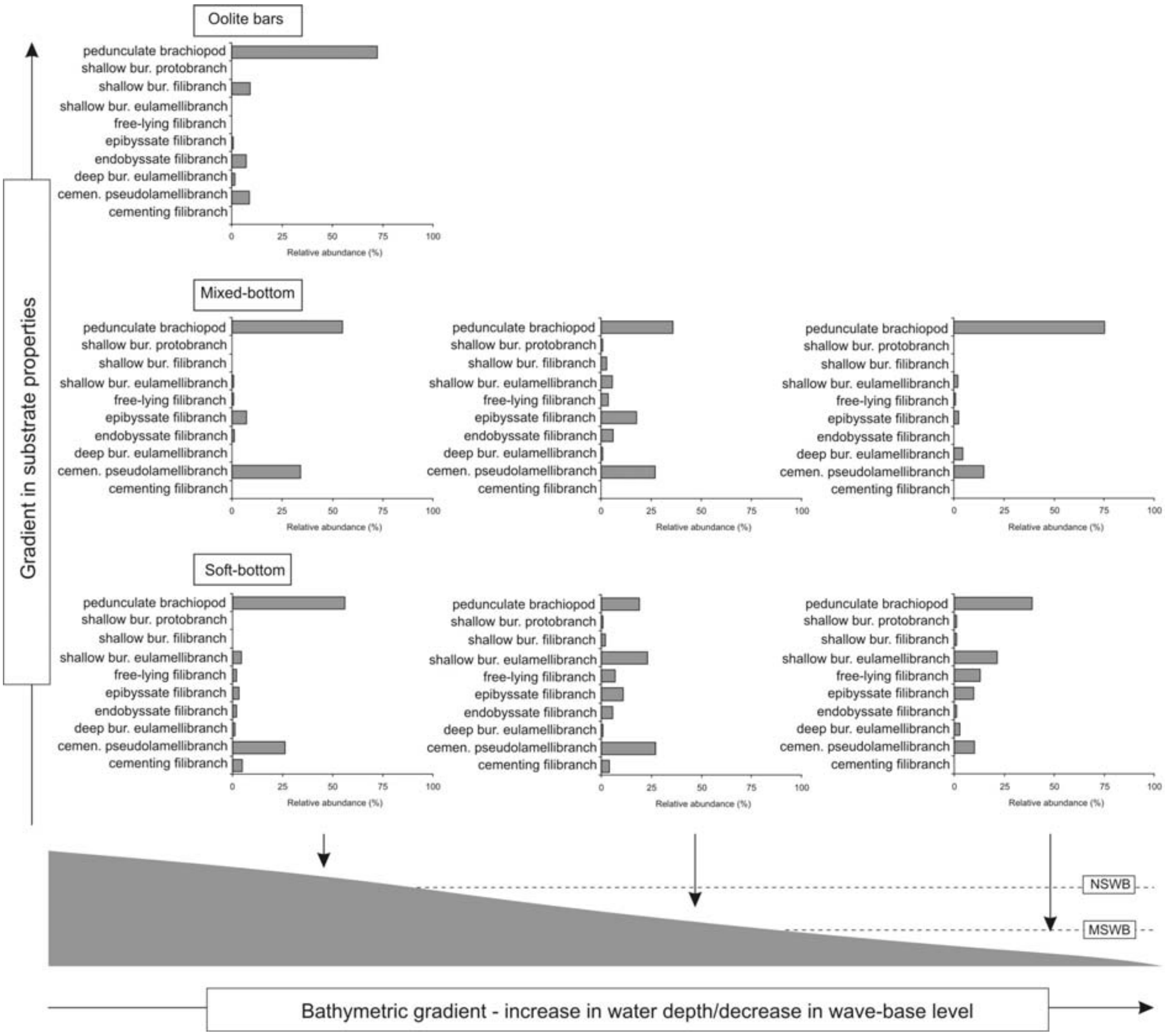


Figure 21 - Differences in guild abundances among habitats with respect to varying wave-base level *and* substrate consistency. Shallow burrowing bivalves decreased and brachiopods increased in abundance towards habitats with higher substrate consistency.

Separation of substrate effects. When substrate is kept constant, the differences among four habitats are significant but relatively low in terms of species abundances (R = 0.17, p < 0.0001). The similar result follows for guild abundances, although the differences among habitats are lower (R = 0.07, p = 0.017). In terms of species abundances, the main differences are related to habitats below MSWB on one hand, and habitats above MSWB and above NSWB on the other hand (Tab. 3). Pedunculate brachiopods and shallow burrowing eulamellibranchs did not consistently varied in abundance among habitats. Cementing pseudolamellibranchs decreased in abundance with increasing depth both on mixed and soft substrates (Fig. 21). Two-way crossed analyses were further restricted to one siliciclastic type. In limestones, the differences among habitats are significant for species abundances (R = 0.37, p < 0.0001) and insignificant for guild abundances (R = -0.01, p = 0.52). In marly limestones, the differences among habitats are minimal but significant for species abundances (R = 0.12, p = 0.02) and guild abundances (R = 0.1, p = 0.025). In marls that represent soft-bottoms only, there are no significant differences in species (R = 0.18, p = 0.067) and guild abundances (R = -0.04, p = 0.57) between habitats above and below MSWB.

Effects of substrate

One-way analyses. The differences in sample-level composition among soft substrates, mixed substrates, and oolite bars are very low although significant for species (R = 0.18, p < 0.0001) and guild abundances (R = 0.07, p =0.009). Pairwise comparisons based on species abundances demonstrate that the main differences are between oolite bars on one hand, and soft and mixed substrates on the other. The differences between soft and mixed substrate is also significant but very low (R = 0.14, p < 0.0001). The pedunculate brachiopods (*Rhactorhynchia* sp. A., *Zeilleria subbucculenta, Stiphrothyris mouterdei*) dominated on oolite bars. In addition to the pedunculate brachiopods, mixed substrates were dominated by cementing pseudolamellibranchs (*Liostrea sandalina, Actinostreon gregareum*) and epibyssate filibranchs (*Arcomytilus, Plagiostoma, Rostroperna*). The pedunculate brachiopods (*Tubithyris chouberti*), shallow burrowing eulamellibranchs (*Nicaniella* sp., *Protocardia (P.)* sp.), cementing pseudolamellibranchs (*Liostrea sandalina*), and free-lying filibranchs (*Entolium (E.) corneolum, E. (Cingentolium)* sp.) were common on soft substrates.

Separation of siliciclastic effects. Allowing for fact that there are siliciclastic effects, two-way ANOSIM shows that there are significant differences in species abundances among three substrates (R = 0.125, p = 0.0001). Between-substrate differences are significant for all three pairwise comparisons, although the main difference is between oolite bars on one hand, and mixed and soft substrates on the other hand (Tab. 4). The differences among substrates in guild abundances are insignificant (R = 0.02, p = 0.22). Limestones were dominated by pedunculate brachiopods and cementing pseudolamellibranchs. Those derived from soft bottoms were dominated by *Tubithyris chouberti* and those derived from mixed bottoms by *Stiphrothyris mouterdei*, *Liostrea sandalina* and *Zeilleria subbucculenta*. Marly limestones were dominated both in soft-bottom and mixed-bottom habitats by *Liostrea sandalina*. Marls, representing soft-bottoms only, were dominated mainly by shallow burrowing eulamellibranchs (*Nicaniella* sp., *Protocardia (Protocardia)* sp., *Mactromya* sp.). In general, abundance of infaunal guilds increased and abundance of cementing guilds and brachiopods decreased towards soft-bottom habitats under conditions affected by some siliciclastic input (i.e., marls and marly limestones, Fig. 18). However, pedunculate brachiopods did not substantially change in abundance towards soft-bottom habitats under carbonate-rich conditions (i.e., limestones). Two-way crossed analyses were further restricted to one habitat type. In habitats below MSWB, the difference between marls and limestones is insignificant for species (R = 0.22, p = 0.063) and guild abundances (R = -0.03, p = 0.56). Similarly, in habitats above MSWB, the difference between marls and limestones is insignificant for species (R = 0.004, p = 0.41) and guild abundances (R = 0.05, p = 0.17). In habitats above NSWB, the difference between marls and marly limestones is insignificant for species (R = 0.18, p = 0.12) and guild abundances (R = -0.09, p = 0.64).

Separation of wave-base level effects. When habitat is kept constant, the differences among three substrates are low and significant for species abundances (R = 0.12, p = 0.013, Tab. 4). This difference is related to pairwise difference between soft and mixed substrates (R = 0.11, p = 0022). The differences among three substrates are insignificant for guild abundances (R = 0, p = 0.46). In habitats above NSWB, soft-bottoms were dominated by *Rugitella prebullata* and *Liostrea sandalina*, mixed-bottoms by L. *sandalina, Stiphrothyris mouterdei* and *Rhactorhynchia* sp. A, and oolite bars by *Rhactorhynchia* sp. A and *Zeilleria subbucculenta*. Pedunculate brachiopods (*Rhactorhynchia* sp. A) decreased in abundance and infaunal bivalves (*Nicaniella* sp.) increased in abundance towards soft-bottoms in habitats above MSWB and below MSWB. Two-way crossed analyses were further restricted to one siliciclastic type. In limestones, the differences among substrates are significant for species abundances (R = 0.28, p = 0.019) and insignificant for guild abundances (R = -0.08, p = 0.69). In marly limestones, the differences among substrates are neither significant for species (R = 0.07, p = 0.18) nor guild abundances (R = 0.01, p = 0.38). Marls are represented by soft substrate only.

One-way ANOSIM	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.176	<0.0001	10000	0
soft-bottom vs. mixed-bottom	0.138	<0.0001	10000	0
soft-bottom vs. ooids	0.366	0.0001	10000	1
mixed-bottom vs. ooids	0.205	0.0062	10000	62
Guilds - global test	0.069	0.0091	10000	91
soft-bottom vs. mixed-bottom	0.09	0.0009	10000	9
soft-bottom vs. ooids	0.049	0.24	10000	2481
mixed-bottom vs. ooids	-0.04	0.63	10000	6322

Two-way ANOSIM (substrate effects, allowing for siliciclastic effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.125	0.0001	10000	1
soft-bottom vs. mixed-bottom	0.087	0.0047	10000	47
soft-bottom vs. ooids	0.487	<0.0001	10000	0
mixed-bottom vs. ooids	0.232	0.0036	10000	36
Guilds - global test	0.018	0.22	10000	2224

Two-way ANOSIM (substrate effects, allowing for habitat effects)	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.123	0.013	10000	126
soft-bottom vs. mixed-bottom	0.11	0.022	10000	221
soft-bottom vs. ooids	-0.107	0.8	15	12
mixed-bottom vs. ooids	0.284	0.062	210	13
Guilds - global test	0	0.46	10000	4594

Table 4 - Analyses of similarities (ANOSIM) testing effects of varying substrate consistency on species and guild composition. This is evaluated with (1) one-way analyses that do not take into account any possible interactions with siliciclastic supply and wave-base level, (2) two-way crossed analyses that keep siliciclastic supply constant, and (3) two-way crossed analyses that keep wave-base level constant. Applying the Bonferroni correction for the pairwise comparisons lowers the alpha value to 0.017 (0.05/3).

Relationship between shell density and bed thickness

Shell density in limestones and marls decreases towards the east. This trend was quantified by measuring the proportion of shell beds thicker than 5 cm (Fig. 22). It is coupled with the increase in water depth towards the east and towards the centre of the Central High Atlas Basin. In the Tidrit section, 54% of limestone beds are densely packed and 22% of limestone beds are loosely packed. In the Talghemt and Kasba Flilo sections, 23% of limestone beds are densely packed and 19% of limestone beds are loosely packed. In the Bou Kendill and Assemaur sections, 1% of limestone beds are densely packed and 22% of limestone beds are loosely packed (Fig. 22). 17% of marls are densely packed and 26% of marls are loosely packed in the Tidrit section. 1% of marls are loosely packed in the Talghemt and Kasba Flilo sections. 1% of marls are densely packed and 4% are loosely packed in the Bou Kendill and Assameur sections. Thickness of marl beds substantially increases towards the east and towards the centre of the Central High Atlas Basin (Fig. 23A). Marls are significantly thicker near the northeastern margin of the basin (Talghemt and Kasba Flilo sections, mean = 165 cm) and in the basin centre (Bou Kendill and Assameur sections, mean = 188 cm) than in southwestern part of the basin (Tidrit section, mean = 49 cm). The differences in the thickness of limestone beds are relatively subtle among the Tidrit section (mean = 16 cm), Talghemt and Kasba Flilo sections (mean = 19 cm), and Bou Kendill and Assameur sections (mean = 21 cm), although limestone beds slightly increase in thickness towards the east. In terms of relationship between shell density and bed thickness, limestones with varying shell density do not show any differences in the thickness in the Tidrit section, and in the Bou Kendill and Assameur sections (Fig. 23B). In the Talghemt and Kasba Flilo sections, shell density increases with increasing thickness of limestone beds (Fig. 23B). Thicker marls are characterized by lower shell density in the Tidrit section, and in the Bou Kendill and Assameur sections (Fig. 23C).

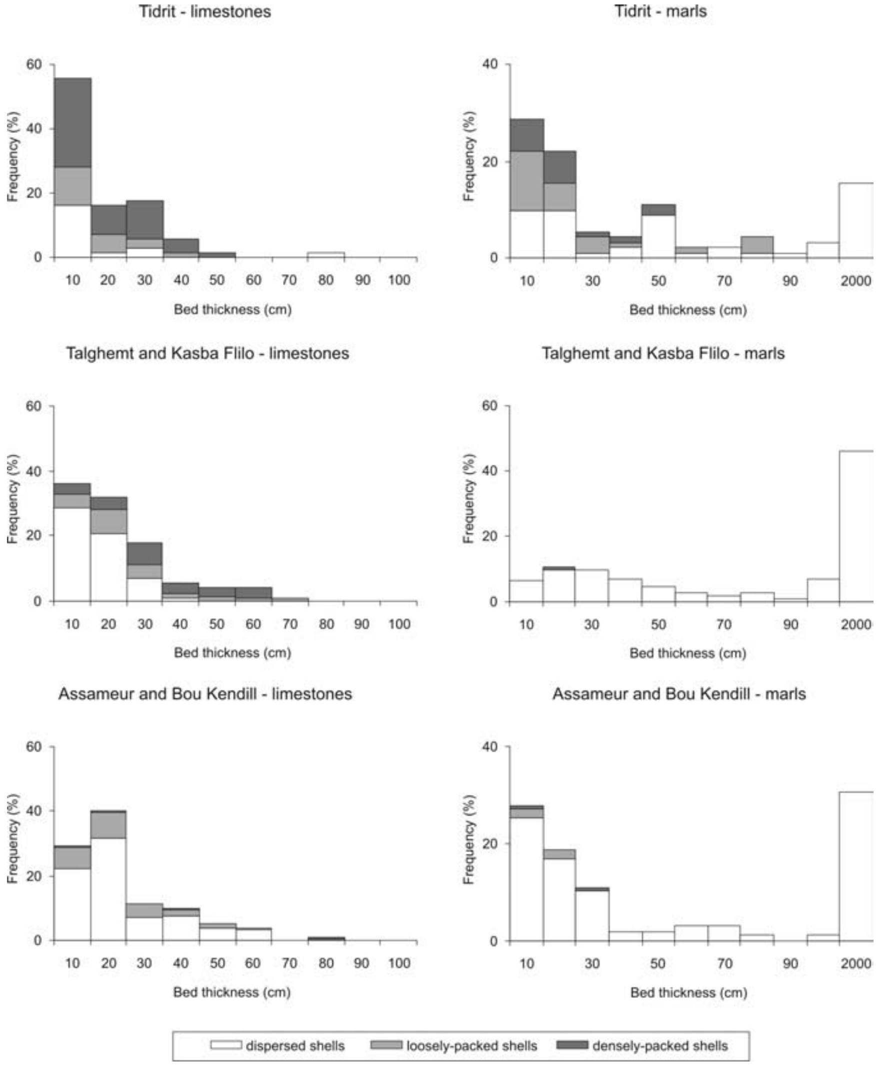


Figure 22 - Thickness-frequency distributions of limestones and marls with varying shell density evaluated separately for shallow habitats (Tidrit), habitats intermediate in depth (Talghemt and Kasba Flilo), and deep habitats (Bou Kendill and Assameur). Note that proportions of densely and loosely packed beds decreases with depth. This pattern holds true both for limestones and marls.

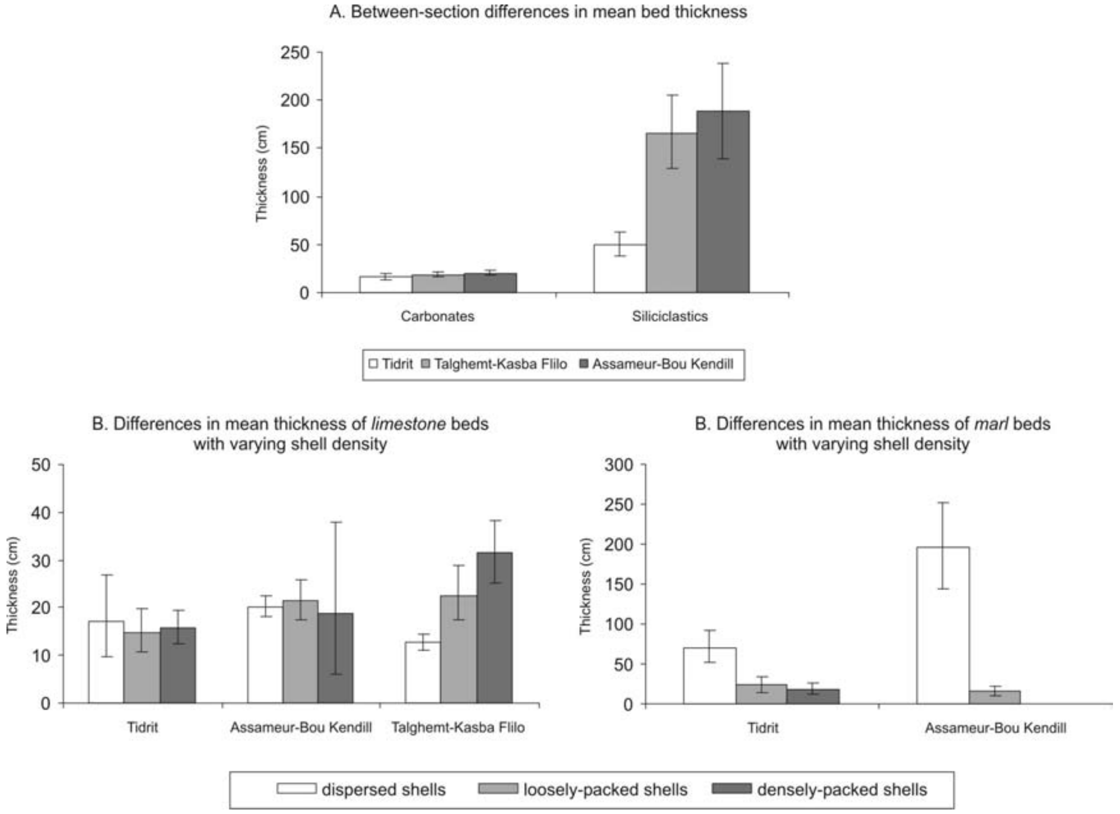


Figure 23 - A. Changes in mean thickness of limestones and marls with increasing depth. The mean values with 95% bootstrapped confidence intervals are shown. Limestone beds showed a very slight increase in thickness with increasing depth. Marls were characterized by a substantially higher thickness in deep than in shallow habitats. B. Differences in mean thickness among limestone beds differing in the shell density are very low and insignificant within sections. In the Talghemt and Kasba Flilo sections, the shell density increases with the increasing bed thickness. C. Differences in mean thickness among marls differing in the shell density show that the shell density decreased with the increasing bed thickness.

Discussion

Taphonomic effects

Taphonomic effects of preferential shell destruction of aragonitic, mostly infaunal bivalves and/or lower sampling probability of molds in lithified limestones may lead to overdominance of brachiopods and calcitic, mostly epifaunal bivalves. Sanders (2003) described possible pathways that lead to syndepositional dissolution of aragonitic shells in carbonate environments. Two arguments are proposed here that this bias should not account for the observed abundance of brachiopods and calcitic bivalves in limestones. First, as any dissolution sequence proceeds in time, shells in a fossil assemblage should exhibit variable states of dissolution. However, the proportion of dissolved shells of originally aragonitic mollusks in thin-sections of limestone beds is very low. Second, only samples that contained gastropods or small corals as possible taphonomic control groups for aragonitic bivalves were analyzed.

Effect of environmental factors on relative abundances

Temporal variations in community composition indicate that there was some within-habitat species replacement, but guild abundances did not substantially change within habitats in time. This implies that there were no abrupt or substantial biotic transitions (e.g., out-of-basin immigrations or large-scale, regional extinctions) within the observed time interval and within the area of the Central High Atlas Basin. Abundances of brachiopod and bivalve guilds were thus probably mainly governed by their response to fluctuations in local environmental factors, either via continuous habitat tracking, or via relatively rapid basin-scale immigration of species that had source populations in other parts of the basin.

The separation of wave-base level and substrate effects from effects of siliciclastic supply is crucial because any segregation between communities dominated by epifaunal brachiopods and infaunal bivalves might be driven by substrate properties because of their differential substrate preferences (Fürsich, 1976; Thayer, 1983). The substrate consistency commonly co-varies positively with a decrease in depth and an increase in siliciclastic supply. Therefore, any difference in community composition among habitats differing in wave-base level, and among habitats differing in the siliciclastic supply might be related to substrate differences. In the Central High Atlas Basin, differential distribution of brachiopods and bivalves with respect to varying carbonate and siliciclastic sedimentation holds true when wave-base level and substrate consistency are kept constant. The effects of varying siliciclastic supply on guild abundances were substantially higher than the effects of wave-base level and substrate. In addition, the latter two factors showed mainly effects on species abundances and affected guild abundances only in interaction with siliciclastic supply. It is thus suggested that physical niches of brachiopods and bivalves were partly segregated in the Central High Atlas Basin and that this segregation was mainly related to their different requirements to variations in siliciclastic supply, turbidity, and land-derived food supply.

This scenario is in accord with the prior hypothesis that follows from actualistic distribution patterns and experimental observations about feeding ecology of brachiopods and bivalves. Present-day brachiopods and bivalve differ in feeding strategies and have different abilities to cope with varying food supply and turbidity levels (Rhodes and Thayer, 1991; Rhodes and Thompson, 1992, 1993; James et al., 1992). Feeding rates of rhynchonellid and terebratulid brachiopods are more inhibited by high particle concentrations than feeding rates of bivalves. Therefore, reduced abundance of brachiopods in marls was probably related to negative effects of high turbidity levels. With respect to food supply requirements, brachiopods are commonly abundant in present-day habitats with reduced or fluctuating food supply. They have low metabolic demands and maximize efficiency of water transport during feeding (LaBarbera, 1981b). Suspension-feeding bivalves have higher metabolic demands and thus higher food supply requirements than brachiopods. Filibranch and pseudolamellibranch bivalves have relatively high clearance rates and can be well adapted to conditions with reduced food supply. Abundance of filibranch (*Entolium*) and pseudolamellibranch bivalves (*Liostrea*) both in limestones and marls points to their wide niche breadth with respect to food supply and turbidity levels. Lower feeding efficiency of eulamellibranch bivalves with high metabolic rates can be the explanation for their decrease in abundance in carbonate-rich habitats with reduced food supply. Reduced levels of turbidity and food supply during carbonate-rich conditions are also indicated by local growth of coral patch-reefs that laterally pass into limestone beds with level-bottom fauna of brachiopods and epifaunal bivalves in the lower parts of the Assameur section.

Analyses of fossil assemblages also showed that brachiopods reached abundance peaks in environments with restricted turbidity and siliciclastic supply, in contrast to communities dominated by bivalves. This pattern was observed in the Toarcian of the southwestern Europe (Fürsich et al., 2001), in the Middle Jurassic of the western India (Fürsich et al., 2004b), and in the Upper Triassic of the Eastern Alps (Tomašových, 2006b). Variations in siliciclastic/carbonate supply and food supply had also substantial effects on distribution and abundance of fossil bivalves (Miller, 1988; Miller and Connolly, 2001; Novack-Gottshall and Miller, 2003a, b).

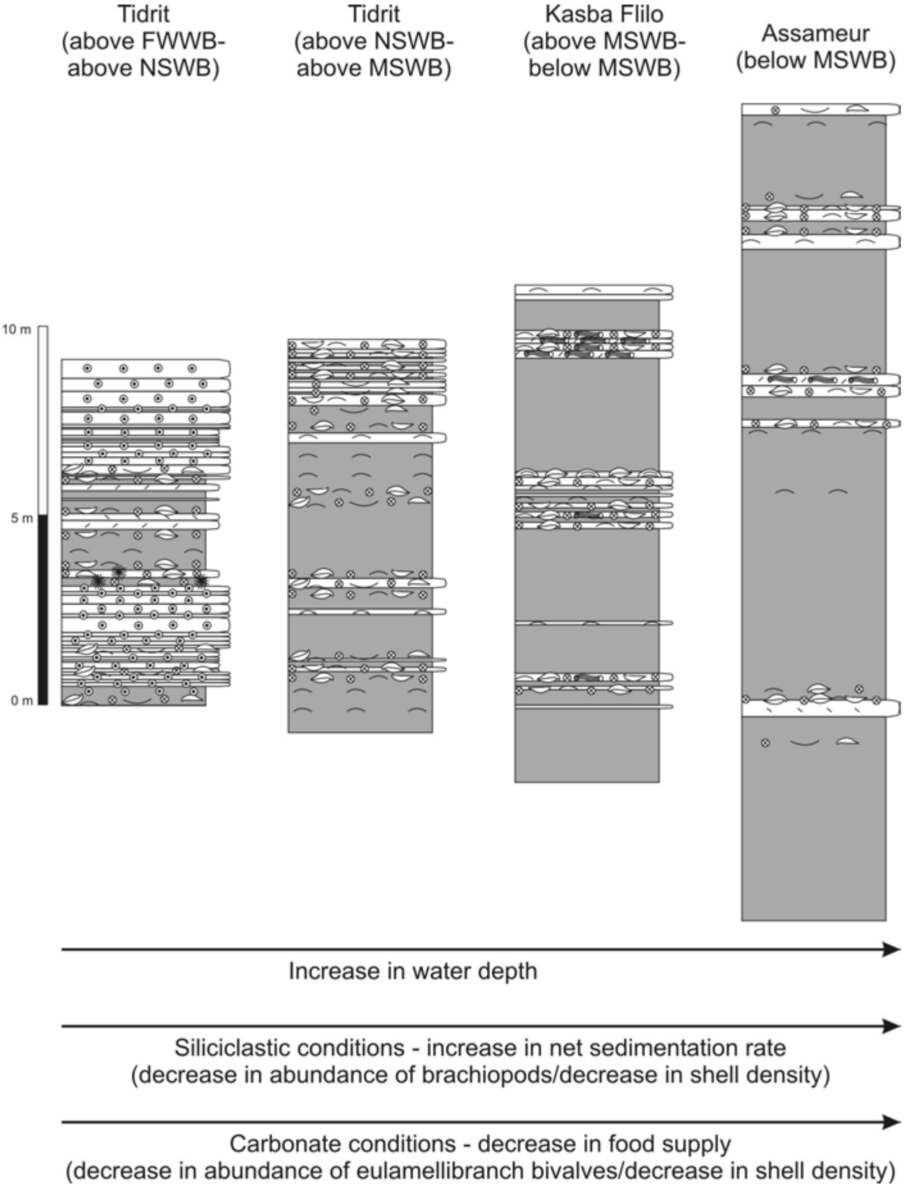


Figure 24 - Simplified scenario showing effects of siliciclastic and food supply on thickness, shell density and community composition of marls and limestones with increasing depth.

Effects of environmental factors on shell density

In general, the decrease in bed thickness towards the deeper parts of the basin implies that net sedimentation rate increased with depth. The proximity and amount of siliciclastic supply probably did not allow the formation of sediment-starved deposits in offshore environments of the Central High Atlas Basin. Negative correlation between shell density and bed thickness in *marls* is in accord with the expectation that higher sedimentation rates dilute and thus decrease shell density. Therefore, with increasing rate of siliciclastic sedimentation towards the east and with increasing depth, shell density of death assemblages was probably reduced by effects of sediment dilution, and by inhibitory effects on ecology of shell-producers, thus decreasing their population density and input of dead shells into the death assemblage. This explanation is also in accord with the ecologic explanation of higher abundance of bivalves in marls because of their higher tolerance to high sedimentation rate and turbidity when compared to pedunculate brachiopods (Fig. 24).

In contrast, shell density does not decrease with increasing bed thickness of *limestones*. This implies that the reduced shell density of limestone beds towards the east and with the increasing water depth was not caused by increasing net rate of sedimentation leading to dilution of shells. The decrease in shell density was probably caused by ecologic factors that decreased rates of dead-shell production. These factors might be related to decreased food supply owing to decreased input of siliciclastic supply and land-derived nutrients. With this reasoning, decreasing shell density with increasing depth during deposition of limestone beds was related to a decrease in food supply rather than to increase in sedimentation rate. This idea is in accord with the suggestion that reduced abundance of infaunal bivalves and dominance of brachiopods in soft-bottom, carbonate-rich habitats reflects conditions with reduced food supply (Fig. 24).

Conclusions

Benthic communities dominated by brachiopods and infaunal, mainly eulamellibranch bivalves inhabiting the Central High Atlas Basin during the Early Bajocian were mainly separated along a gradient with varying siliciclastic and food supply. Relative abundances of pedunculate brachiopods decreased and relative abundance of shallow burrowing bivalves increased with increasing rate of siliciclastic and food supply. This gradient is not conflated by effects of substrate consistency and wave-base level because variations in siliciclastic supply showed significant effects on species and guild abundances even when wave/base level and substrate type were kept constant. Variations in wave-base level and substrate consistency had significant effects on guild abundances only in interaction with siliciclastic supply. Epifaunal, mainly filibranch and pseudolamellibranch bivalves had probably wide niche tolerance with respect to varying food and siliciclastic supply. This pattern is in accord with the hypothesis that pedunculate brachiopods and infaunal bivalves were characterized by partly segregated physical niches with respect to siliciclastic and food supply gradient. The effects of siliciclastic supply and the effect of food supply on ecology of brachiopods and bivalves are supported by depth-related trend in shell density of fossil assemblages. Shell density of marls and limestones decreased with increasing depth and increasing siliciclastic supply towards the east in the Central High Atlas Basin. Shell density negatively correlated with bed thickness of marls, showing that higher net sedimentation rates controlled shell density via dilution or inhibition of shell producers. Poor differences in thickness among limestone beds differing in the shell density imply that the depth-related decrease in shell density of limestones was not governed by net sedimentation rate alone, but might be related to the decrease in food supply owing to reduced input of land-derived nutrients. Variations in relative abundances and shell density of brachiopods and bivalves are thus explained by effects of (1) sedimentation rate and particle concentrations that increased in magnitude during siliciclastic conditions, thus reducing abundance of brachiopods, and (2) food supply that decreased in abundance during carbonate-rich conditions, thus abundance of shallow burrowing bivalves.

	JA1	JA1.3	JA1.4	JA1.5	JA1.6	JA1.7	JA1.8	JA4.4	JA4.5	JA1-5	JA2-5	JA2-5.2	JA6	JA7	JA8	JA9	JA10	JA11	JA12
Rhactorhynchia sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubithyris chouberti	43	3	0	0	0	0	21	5	0	4	3	0	24	0	0	59	62	54	13
Stiphrothyris mouterdei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rugitella prebullata	0	19	0	2	0	7	0	17	0	7	0	16	0	0	0	0	0	0	0
Zeilleria subbucculenta	0	39	0	57	0	10	0	15	2	25	8	17	0	0	0	2	1	2	0
Rhynchonellid sp. A	0	4	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liostrea sandalina	16	4	0	16	3	14	5	2	16	23	9	8	8	2	15	2	0	1	12
Nanogyra nana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudolimea sp.	2	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Entolium) corneolum	0	0	0	0	0	0	0	0	0	0	0	0	34	0	0	26	0	0	0
Chlamys (Chlamys) sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Camptonectes (Camptonectes) auritus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0
?*Camptonectes (Camptochlamys)* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Cosmetodon) sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp. B	0	0	5	7	12	2	1	4	0	3	0	0	1	5	0	0	1	2	5
Isognomon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillaria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillia (Cultriopsis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Costigervillia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bakevellia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp.	1	0	0	0	0	0	0	0	5	5	0	0	0	0	0	0	0	0	0
Tancredia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	0	0	2	1	0	0	0	0	0	0	0	0	0	8	7	0	0	0	1
Anisocardia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. C	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella sp.	0	0	83	17	1	0	2	0	0	0	0	0	0	2	5	0	0	0	9
?*Coelastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Pressastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Bositra sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	1	0	0	0	0	0	0	0	0	4	2	1	0	0	0	0	0	0
Mactromyopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mactromya sp.	0	0	1	4	9	0	1	0	2	3	0	0	0	1	1	0	0	0	0
Corbulomima sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rostroperna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont sp. A (elongate)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont sp. B (oval)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opis (Trigonopis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Ceratomyopsis* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Pholadomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Bucardiomya) sp.	4	0	0	0	0	0	9	0	2	1	0	0	4	0	0	6	0	2	0
Prorokia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonoastarte sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?Inoceramid sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Rollieria* sp.	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. B	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Acanthothiris sp.	0	0	0	0	0	0	1	0	0	0	0	0	7	0	1	9	7	3	12
Pleuromya uniformis	0	0	0	0	0	0	9	0	0	0	0	0	10	0	0	1	0	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Vaugonia (?Orthotrigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Trigonia (Trigonia) sp. C	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Entolium (Cingentolium) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Eocallista* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kallirhynchia aff. *oranensis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liostrea sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichites sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Plectomya* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 – Absolute abundances of brachiopod and bivalve species

	JA12.2	JA14	JA14.4	JA15	JA16	JA16.2	JA18	JA18.2	JA20	JA22	JA23	JA28	JA29	JK77	JK4	JK5	JK5.2	JK5.5	JK5.6
Rhactorhynchia sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	271	0	0	0	0	0
Tubithyris chouberti	50	44	9	22	4	0	5	0	0	0	25	6	0	0	0	0	0	0	0
Stiphrothyris mouterdei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rugitella prebullata	0	1	1	0	3	0	0	0	0	0	0	10	5	0	20	15	0	15	9
Zeilleria subbucculenta	0	0	0	0	0	0	12	11	0	6	0	0	0	4	4	13	25	23	13
Rhynchonellid sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Liostrea sandalina	2	8	3	2	3	0	3	13	0	12	0	0	0	0	0	0	11	0	0
Nanogyra nana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudolimea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Entolium) corneolum	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0
Chlamys (Chlamys) sp.	0	0	0	0	0	0	0	0	0	0	0	5	3	0	0	0	0	0	0
Camptonectes (Camptonectes) auritus	0	0	0	0	1	0	0	0	0	0	0	1	1	10	0	0	0	0	0
?*Camptonectes (Camptochlamys)* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Cosmetodon) sp.	0	0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	0
Grammatodon (Grammatodon) sp. B	0	3	2	4	2	6	1	0	1	0	0	0	0	0	0	0	0	0	0
Isognomon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillaria sp.	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Gervillia (Cultriopsis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Costigervillia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bakevellia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratomya sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tancredia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	1	0	5	0	2	1	0	0	0	5	0	0	0	2	0	0	0	0	0
Anisocardia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. C	0	0	0	0	0	0	0	0	0	0	0	7	0	1	0	0	0	0	0
Nicaniella sp.	0	1	16	6	0	9	0	42	0	5	0	0	0	0	0	0	0	0	0
?*Coelastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Pressastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Bositra sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Mactromyopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mactromya sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Corbulomima sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rostroperna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont sp. A (elongate)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont sp. B (oval)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opis (Trigonopis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Ceratomyopsis* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Pholadomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Bucardiomya) sp.	0	4	0	0	0	0	1	0	0	2	1	2	0	0	0	0	0	0	0
Prorokia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonoastarte sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?Inoceramid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Rollieria* sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthothiris sp.	3	4	2	0	3	0	13	1	22	2	0	0	0	0	0	0	0	0	0
Pleuromya uniformis	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Vaugonia (?Orthotrigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. C	1	0	1	2	1	1	0	3	0	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Cingentolium) sp.	0	0	3	2	15	17	15	9	8	1	0	0	0	0	0	0	0	0	0
?*Eocallista* sp.	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Kallirhynchia aff. *oranensis*	0	0	0	0	0	0	0	0	0	0	2	20	3	0	0	0	0	0	0
Liostrea sp. A	0	0	0	0	0	0	0	0	0	0	0	15	22	0	0	0	0	0	0
Trichites sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
?*Plectomya* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) – Absolute abundances of brachiopod and bivalve species.

	JK8	JK9.2	JK15	JK20.4	JK24.9	JK32	JK33	KF1-1	KF1-2	KF1-3	KF1	KF2	KF2.8	KF3	KF3.2	KF3.4	KF4	KF4.5	KF5
Rhactorhynchia sp. A	0	6	0	0	0	0	0	0	0	0	0	0	5	17	0	0	34	1	14
Tubithyris chouberti	1	0	0	32	0	3	0	10	9	0	0	0	0	0	0	0	0	0	0
Stiphrothyris mouterdei	0	0	0	0	0	0	0	0	0	21	0	0	17	13	0	0	7	2	3
Rugitella prebullata	0	0	0	0	69	21	26	1	0	0	0	0	1	23	0	0	3	1	0
Zeilleria subbucculenta	0	8	16	0	17	0	1	7	1	0	0	0	0	0	0	0	0	0	1
Rhynchonellid sp. A	0	0	1	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	4	0
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1
Liostrea sandalina	0	3	10	0	0	5	2	0	2	0	0	0	16	23	0	0	43	5	5
Nanogyra nana	0	0	0	0	0	0	0	0	5	0	0	0	10	13	0	0	10	0	15
Pteria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudolimea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Entolium) corneolum	3	0	2	0	0	3	0	0	1	0	0	0	0	4	0	1	8	24	11
Chlamys (Chlamys) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Camptonectes (Camptonectes) auritus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
?*Camptonectes (Camptochlamys)* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Cosmetodon) sp.	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp. B	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isognomon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillaria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillia (Cultriopsis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Costigervillia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bakevellia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Ceratomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Tancredia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	1	18	0	0	0	0	0	0	0	0	5	0	0	0	1	2	0	5	0
Anisocardia sp.	0	0	0	0	0	0	0	0	0	0	0	9	0	0	2	0	0	0	0
Plagiostoma sp. A	0	0	0	0	0	0	0	1	10	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella sp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	14	8	2	0	1
?*Coelastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Pressastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	0	1	0	0	1	0	0	0	1	0	0	0	3	2	0	0	0	0	0
Bositra sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Actinostreon gregareum	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Mactromyopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mactromya sp.	6	1	1	0	0	0	0	0	0	0	8	3	0	0	0	0	0	0	0
Corbulomima sp.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	0	0
Trigonia (Trigonia) sp. A	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Trigonia (Trigonia) sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Rostroperna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont sp. A (elongate)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont sp. B (oval)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opis (Trigonopis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Ceratomyopsis* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Pholadomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Bucardiomya) sp.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Prorokia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonoastarte sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
Nuculoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?Inoceramid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Rollieria* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. B	0	0	0	0	0	0	0	2	4	2	0	0	4	0	0	0	0	0	0
Acanthothiris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya uniformis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaugonia (?Orthotrigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	1	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Trigonia (Trigonia) sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0
Entolium (Cingentolium) sp.	0	0	0	0	0	0	0	0	0	0	11	15	0	0	6	0	0	0	0
?*Eocallista* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kallirhynchia aff. *oranensis*	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0
Liostrea sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichites sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Plectomya* sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) - Absolute abundances of brachiopod and bivalve species.

	KF5.11	KF6	KF7	KF17.2	KF18.2	TT1	TT1.3	TT2	TT3	TT3.5	TT3.7	TT3.9	TT4	TT7	TT8	TT11	TT14	BT1	BT1.2
Rhactorhynchia sp. A	5	113	30	0	0	0	1	0	0	2	9	0	0	0	0	0	0	17	20
Tubithyris chouberti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stiphrothyris mouterdei	0	14	3	2	0	0	0	0	9	86	44	0	0	30	22	5	8	0	0
Rugitella prebullata	0	1	3	77	16	0	0	0	9	0	7	0	1	4	0	0	0	0	0
Zeilleria subbucculenta	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	10	16	0	0
Rhynchonellid sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	19	4
Liostrea sandalina	9	45	29	60	38	9	26	6	17	12	14	0	4	4	15	1	3	3	2
Nanogyra nana	0	12	23	0	0	10	25	0	0	0	0	0	1	2	17	0	0	0	0
Pteria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	14
Placunopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Pseudolimea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Entolium) corneolum	7	1	1	0	0	20	3	12	0	0	0	20	12	0	2	3	0	0	0
Chlamys (Chlamys) sp.	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	9	1	0	0
Camptonectes (Camptonectes) auritus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4
?*Camptonectes (Camptochlamys)* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Cosmetodon) sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	2	1
Grammatodon (Grammatodon) sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isognomon sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillaria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Gervillia (Cultriopsis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Costigervillia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Bakevellia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Ceratomya sp.	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pinna sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Tancredia sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1
Protocardia (Protocardia) sp.	2	2	2	0	0	0	0	0	0	0	0	0	2	1	3	0	0	0	6
Anisocardia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Plagiostoma sp. A	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Plagiostoma sp. C	0	0	0	0	0	3	0	0	0	0	0	0	1	0	0	8	1	0	0
Nicaniella sp.	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	2	0
?*Coelastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Pressastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bositra sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mactromyopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mactromya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Corbulomima sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Rostroperna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont sp. A (elongate)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont sp. B (oval)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Opis (Trigonopis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Ceratomyopsis* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Pholadomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Bucardiomya) sp.	0	4	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Prorokia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonoastarte sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?Inoceramid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Rollieria* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthothiris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya uniformis	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaugonia (?Orthotrigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Cingentolium) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
?*Eocallista* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kallirhynchia aff. *oranensis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	20	0	0
Liostrea sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichites sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Plectomya* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) - Absolute abundances of brachiopod and bivalve species.

	BT1.3	BT1.4	BT4	BT07	BT09b	BT10-1	BT10-2	BT14	BT19.2	BT25.2	BT37.2	BT38.5	BT39.4	BT40b	BT48.2	BT50	BT50.6	BT51.3	BT51.4
Rhactorhynchia sp. A	41	0	6	11	22	0	14	0	0	0	0	0	0	0	1	40	52	7	0
Tubithyris chouberti	0	0	0	0	0	0	2	6	0	0	2	0	2	0	0	0	0	0	0
Stiphrothyris mouterdei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rugitella prebullata	0	0	0	0	0	0	0	7	0	0	4	0	0	0	0	0	0	0	0
Zeilleria subbucculenta	0	0	0	0	36	7	0	0	7	10	0	0	0	0	0	1	0	0	0
Rhynchonellid sp. A	0	0	0	0	0	0	0	0	12	9	0	0	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	8
Modiolus sp.	12	1	4	0	4	0	2	0	0	0	1	0	1	0	2	1	0	0	0
Liostrea sandalina	1	3	21	21	7	22	18	67	102	28	14	3	29	12	14	20	9	59	15
Nanogyra nana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria sp.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	2
Pseudolimea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Entolium (Entolium) corneolum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys (Chlamys) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Camptonectes (Camptonectes) auritus	0	12	3	1	0	0	1	2	0	0	0	2	0	0	0	3	0	0	0
?*Camptonectes (Camptochlamys)* sp.	0	0	0	0	0	5	0	0	0	0	0	0	2	0	0	0	0	0	0
Grammatodon (Cosmetodon) sp.	0	1	0	2	0	0	3	0	0	2	3	0	0	0	0	0	0	8	15
Grammatodon (Grammatodon) sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isognomon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillaria sp.	0	0	2	2	0	2	3	0	0	0	0	0	0	1	0	0	0	0	0
Gervillia (Cultriopsis) sp.	0	0	0	0	0	0	0	0	0	0	3	0	0	2	0	0	0	0	0
Costigervillia sp.	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0
Bakevellia sp.	27	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ceratomya sp.	0	2	0	0	0	0	0	1	0	0	1	2	2	0	0	1	0	0	0
Pinna sp.	0	0	4	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0
Tancredia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	0	23	0	0	0	0	10	1	0	0	2	3	0	0	1	0	0	0	0
Anisocardia sp.	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	11
Plagiostoma sp. A	0	1	0	0	1	2	1	0	0	0	0	0	1	0	0	0	0	0	1
Plagiostoma sp. C	0	0	0	4	0	0	0	1	1	4	0	0	4	0	0	0	1	0	0
Nicaniella sp.	0	24	1	0	0	0	24	0	1	1	3	1	0	5	0	0	1	36	28
?*Coelastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Pressastarte* sp.	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	1	0	1	0	8	2	0	6	0	4	4	0	0	1	0	0
Bositra sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	1	0	0	0
Mactromyopsis sp.	0	0	0	0	0	1	2	0	0	2	0	0	2	0	7	0	0	0	0
Mactromya sp.	0	0	0	2	0	0	0	0	0	1	8	21	0	0	0	0	0	5	0
Corbulomima sp.	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. A	0	0	0	0	0	0	4	0	0	0	2	0	4	0	0	0	0	0	0
Trigonia (Trigonia) sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	3	4
Rostroperna sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	4	31	4	0	0	0
Heterodont sp. A (elongate)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Heterodont sp. B (oval)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Opis (Trigonopis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
?*Ceratomyopsis* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pholadomya (Pholadomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pholadomya (Bucardiomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prorokia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonoastarte sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Nuculoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?Inoceramid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Rollieria* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthothiris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya uniformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaugonia (?Orthotrigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Cingentolium) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Eocallista* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kallirhynchia aff. *oranensis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liostrea sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichites sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Plectomya* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) - Absolute abundances of brachiopod and bivalve species.

	BT53	BT53.2	BT53.8	BT54.4	BT54.5	BT54.6	BT56	BT56.3	BT57	BT59.2	BT61	BT64.5	BT67.8	BT67.12	BT77	BT79.2	BT81.2	BT81.4	BT87.6	BT90.3	BT103	BT107	BT109
Rhactorhynchia sp. A	1	9	6	8	15	9	31	13	44	0	4	5	35	68	100	0	68	151	68	18	0	0	0
Tubithyris chouberti	0	0	0	0	0	1	0	5	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stiphrothyris mouterdei	1	36	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	71	30	43	0
Rugitella prebullata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0
Zeilleria subbucculenta	0	0	0	0	0	0	0	2	0	0	0	0	0	0	13	36	0	5	2	0	0	0	53
Rhynchonellid sp. A	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	1	0	2	6	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus sp.	0	0	0	6	18	18	15	10	20	0	0	3	7	0	10	1	0	0	12	0	0	0	0
Liostrea sandalina	9	2	4	20	56	42	17	2	9	5	4	1	18	8	0	2	0	0	14	2	11	14	0
Nanogyra nana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria sp.	0	0	0	0	2	1	3	1	6	0	0	1	0	0	0	0	0	0	0	0	5	0	0
Placunopsis sp.	0	0	0	0	0	0	1	2	1	0	0	96	0	0	0	0	3	1	0	0	0	0	10
Pseudolimea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Entolium) corneolum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys (Chlamys) sp.	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camptonectes (C.) auritus	0	0	0	0	0	1	1	3	0	0	1	0	0	0	2	0	0	10	0	0	3	0	0
?*Camptonectes (Camptochl.)* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Cosmetodon) sp.	0	0	0	1	0	3	12	5	3	2	1	11	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Gramm.) sp. B	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isognomon sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillaria sp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Gervillia (Cultriopsis) sp.	0	0	0	2	6	3	6	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Costigervillia sp.	0	0	0	0	2	2	7	6	6	2	0	0	2	0	0	0	0	0	0	0	0	0	0
Bakevellia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ceratomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tancredia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	0	0	0	0	0	0	2	2	2	0	5	3	0	0	2	0	0	1	0	0	0	0	0
Anisocardia sp.	0	0	0	0	0	0	0	0	2	0	5	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. A	1	6	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. C	0	0	0	9	14	5	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nicaniella sp.	0	0	0	0	4	10	13	19	27	0	15	43	0	0	0	0	0	0	0	0	0	0	0
?*Coelastarte* sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Pressastarte* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	21	25	20	2	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Bositra sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	10	0	0	33	27	13	1	2	0	8	0	0	2	3	1	0	0	0	0	0	0	0	0
Mactromyopsis sp.	0	0	0	0	2	1	37	17	37	5	2	1	10	0	0	0	0	0	0	0	0	0	0
Mactromya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corbulomima sp.	0	0	0	0	0	0	0	1	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. A	0	2	0	5	9	4	0	1	0	5	3	0	0	0	0	11	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. B	0	0	0	3	0	4	14	6	6	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Rostroperna sp.	0	0	0	6	5	5	2	4	8	50	0	0	2	5	0	0	0	0	0	0	0	0	0
Heterodont sp. A (elongate)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Heterodont sp. B (oval)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opis (Trigonopis) sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Ceratomyopsis* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Pholadomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Pholadomya (Bucardiomya) sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Prorokia sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonoastarte sp.	0	0	0	0	0	0	25	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?Inoceramid sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Rollieria* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acanthothiris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya uniformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaugonia (?Orthotrigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Cingentolium) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Eocallista* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kallirhynchia aff. *oranensis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liostrea sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trichites sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Plectomya* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) - Absolute abundances of brachiopod and bivalve species.

	JA1	JA1.3	JA1.4	JA1.5	JA1.6	JA1.7	JA1.8	JA4.4	JA4.5	JA1-5	JA2-5	JA2-5.2	JA6	JA7	JA8	JA9	JA10	JA11	JA12
Plagiostoma sp. D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaeroidothyris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unicardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna khadirensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculana sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon solitarium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osteomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Integricardium* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indocorbula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cercomya (Capillimya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	JA12.2	JA14	JA14.4	JA15	JA16	JA16.2	JA18	JA18.2	JA20	JA22	JA23	JA28	JA29	JK77	JK4	JK5	JK5.2	JK5.5	JK5.6
Plagiostoma sp. D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaeroidothyris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unicardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna khadirensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculana sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon solitarium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osteomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Integricardium* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indocorbula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cercomya (Capillimya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	JK8	JK9.2	JK15	JK20.4	JK24.9	JK32	JK33	KF1-1	KF1-2	KF1-3	KF1	KF2	KF2.8	KF3	KF3.2	KF3.4	KF4	KF4.5	KF5
Plagiostoma sp. D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaeroidothyris sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Unicardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna khadirensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Nuculana sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon solitarium	0	0	0	0	0	0	0	1	2	0	0	0	0	3	0	0	1	1	2
Grammatodon (Grammatodon) sp. A	0	0	0	0	0	0	0	0	0	0	4	4	0	0	4	13	4	29	0
Osteomya sp.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
?*Integricardium* sp.	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	27	0	0
Indocorbula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Cercomya (Capillimya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0

	KF5.11	KF6	KF7	KF17.2	KF18.2	TT1	TT1.3	TT2	TT3	TT3.5	TT3.7	TT3.9	TT4	TT7	TT8	TT11	TT14	BT1	BT1.2
Plagiostoma sp. D	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaeroidothyris sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Unicardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Inoperna khadirensis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Nuculana sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Actinostreon solitarium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Grammatodon (Grammatodon) sp. A	2	0	0	0	0	0	0	0	0	0	0	0	0	2	4	0	0	0	0
Osteomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Integricardium* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indocorbula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cercomya (Capillimya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) - Absolute abundances of brachiopod and bivalve species.

	BT1.3	BT1.4	BT4	BT07	BT09b	BT10-1	BT10-2	BT14	BT19.2	BT25.2	BT37.2	BT38.5	BT39.4	BT40b	BT48.2	BT50	BT50.6	BT51.3	BT51.4
Plagiostoma sp. D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaeroidothyris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unicardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna khadirensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculana sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon solitarium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osteomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Integricardium* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indocorbula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cercomya (Capillimya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	BT53	BT53.2	BT53.8	BT54.4	BT54.5	BT54.6	BT56	BT56.3	BT57	BT59.2	BT61	BT64.5	BT67.8	BT67.12	BT77	BT79.2	BT81.2	BT81.4	BT87.6	BT90.3	BT103	BT107	BT109
Plagiostoma sp. D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphaeroidothyris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unicardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoperna khadirensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculana sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon solitarium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammat.) sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osteomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Integricardium* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indocorbula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cercomya (Capillimya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) - Absolute abundances of brachiopod and bivalve species.

Species	Guild
Acanthothiris sp.	pedunculate brachiopod
Kallirhynchia aff. *oranensis*	pedunculate brachiopod
Rhactorhynchia sp. A	pedunculate brachiopod
Rhynchonellid sp. A	pedunculate brachiopod
Sphaeroidothyris sp.	pedunculate brachiopod
Stiphrothyris mouterdei	pedunculate brachiopod
Tubithyris aff. *wrighti*	pedunculate brachiopod
Tubithyris chouberti	pedunculate brachiopod
Rugitella prebullata	pedunculate brachiopod
Zeilleria subbucculenta	pedunculate brachiopod
Nuculoma sp.	shallow burrowing protobranch
Palaeonucula sp.	shallow burrowing protobranch
Mesosaccella sp.	shallow burrowing protobranch
Nuculana sp.	shallow burrowing protobranch
?*Rollieria* sp.	shallow burrowing protobranch
Grammatodon (Cosmetodon) sp.	endobyssate filibranch
Grammatodon (Grammatodon) sp. A	epibyssate filibranch
Grammatodon (Grammatodon) sp. B	epibyssate filibranch
Arcomytilus sp.	epibyssate filibranch
Inoperna khadirensis	endobyssate filibranch
Modiolus sp.	endobyssate filibranch
Pteria sp.	epibyssate filibranch
Bakevellia sp.	epibyssate filibranch
Costigervillia sp.	epibyssate filibranch
Gervillaria sp.	epibyssate filibranch
Gervillella sp.	endobyssate filibranch
Gervillia (Cultriopsis) sp.	epibyssate filibranch
Isognomon sp.	epibyssate filibranch
Rostroperna sp.	epibyssate filibranch
Bositra sp.	free-lying filibranch
Oxytoma sp.	epibyssate filibranch
?Inoceramid sp.	epibyssate filibranch
Pinna sp.	endobyssate filibranch
Trichites sp.	endobyssate filibranch
Entolium (Cingentolium) sp.	free-lying filibranch
Entolium (Entolium) corneolum	free-lying filibranch
?*Camptonectes (Camptochlamys)* sp.	epibyssate filibranch
Camptonectes (Camptonectes) auritus	epibyssate filibranch
Chlamys (Chlamys) sp.	epibyssate filibranch
Eopecten sp.	epibyssate filibranch
Plicatula sp.	cementing filibranch
Placunopsis sp.	cementing filibranch
Ctenostreon sp.	free-lying filibranch
Limatula sp.	epibyssate filibranch
Plagiostoma sp. A	epibyssate filibranch
Plagiostoma sp. B	epibyssate filibranch
Plagiostoma sp. C	epibyssate filibranch
Plagiostoma sp. D	epibyssate filibranch
Pseudolimea sp.	epibyssate filibranch
Nanogyra nana	cementing pseudolamellibranch
Liostrea sandalina	cementing pseudolamellibranch
Liostrea sp. A	cementing pseudolamellibranch
Actinostreon gregareum	cementing pseudolamellibranch
Actinostreon solitarium	cementing pseudolamellibranch
Trigonia (Trigonia) sp. A	shallow burrowing filibranch

Supplement 2 – Guild assignments of brachiopod and bivalve species.

Species	Guild
Trigonia (Trigonia) sp. B	shallow burrowing filibranch
Trigonia (Trigonia) sp. C	shallow burrowing filibranch
Vaugonia (?Orthotrigonia) sp.	shallow burrowing filibranch
Mactromya sp.	shallow burrowing eulamellibranch
Mactromyopsis sp.	shallow burrowing eulamellibranch
Unicardium sp.	shallow burrowing eulamellibranch
?*Coelastarte* sp.	shallow burrowing eulamellibranch
Nicaniella sp.	shallow burrowing eulamellibranch
Opis (Trigonopis) sp.	shallow burrowing eulamellibranch
?*Pressastarte* sp.	shallow burrowing eulamellibranch
Prorokia sp.	shallow burrowing eulamellibranch
Trigonoastarte sp.	shallow burrowing eulamellibranch
?*Integricardium* sp.	shallow burrowing eulamellibranch
Protocardia (Protocardia) sp.	shallow burrowing eulamellibranch
Tancredia sp.	shallow burrowing eulamellibranch
Anisocardia sp.	shallow burrowing eulamellibranch
?*Ceratomyopsis* sp.	shallow burrowing eulamellibranch
?*Eocallista* sp.	shallow burrowing eulamellibranch
Heterodont sp. A (elongate)	shallow burrowing eulamellibranch
Heterodont sp. B (oval)	shallow burrowing eulamellibranch
Corbulomima sp.	shallow burrowing eulamellibranch
Indocorbula sp.	shallow burrowing eulamellibranch
Osteomya sp.	deep burrowing eulamellibranch
Pholadomya (Bucardiomya) sp.	deep burrowing eulamellibranch
Pholadomya (Pholadomya) sp.	deep burrowing eulamellibranch
Ceratomya sp.	deep burrowing eulamellibranch
Pleuromya uniformis	deep burrowing eulamellibranch
Cercomya (Capillimya) sp.	deep burrowing eulamellibranch
?*Plectomya* sp.	deep burrowing eulamellibranch
Thracia sp.	deep burrowing eulamellibranch

Supplement 2 (cont.) – Guild assignments of brachiopod and bivalve species.

Sample	Section	Member	Carbonate-siliciclastics	Wave-base level	Substrate	Sample group
JA1	Assameur	middle	limestone	below MSWB	soft-bottom	*Tubithyris chouberti*
JA1.3	Assameur	middle	limestone	below MSWB	mixed-bottom	*Zeilleria subbuculenta*
JA1.4	Assameur	middle	marl	below MSWB	soft-bottom	*Nicaniella*
JA1.5	Assameur	middle	limestone	below MSWB	soft-bottom	*Zeilleria subbuculenta*
JA1.6	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Mactromya*
JA1.7	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Zeilleria subbuculenta*
JA1.8	Assameur	middle	limestone	below MSWB	mixed-bottom	*Tubithyris chouberti*
JA4.4	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Zeilleria subbuculenta*
JA4.5	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Liostrea sandalina*
JA1-5	Assameur	middle	limestone	below MSWB	soft-bottom	*Zeilleria subbuculenta*
JA2-5	Assameur	middle	limestone	below MSWB	mixed-bottom	*Zeilleria subbuculenta*
JA2-5.2	Assameur	middle	limestone	below MSWB	mixed-bottom	*Zeilleria subbuculenta*
JA6	Assameur	middle	limestone	below MSWB	soft-bottom	*Entolium*
JA7	Assameur	middle	marl	below MSWB	soft-bottom	*Protocardia*
JA8	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Liostrea sandalina*
JA9	Assameur	middle	limestone	below MSWB	soft-bottom	*Tubithyris chouberti*
JA10	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Tubithyris chouberti*
JA11	Assameur	middle	limestone	below MSWB	soft-bottom	*Tubithyris chouberti*
JA12	Assameur	middle	limestone	below MSWB	soft-bottom	*Nicaniella*
JA12.2	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Tubithyris chouberti*
JA14	Assameur	middle	limestone	below MSWB	soft-bottom	*Tubithyris chouberti*
JA14.4	Assameur	middle	marl	below MSWB	soft-bottom	*Nicaniella*
JA15	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Tubithyris chouberti*
JA16	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Acanthothiris*
JA16.2	Assameur	middle	marl	below MSWB	soft-bottom	*Nicaniella*
JA18	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Acanthothiris*
JA18.2	Assameur	middle	marl	below MSWB	soft-bottom	*Nicaniella*
JA20	Assameur	middle	marly limestone	below MSWB	soft-bottom	*Acanthothiris*
JA22	Assameur	middle	marly limestone	above MSWB	soft-bottom	*Liostrea sandalina*
JA23	Assameur	middle	limestone	below MSWB	soft-bottom	*Tubithyris chouberti*
JA28	Assameur	upper	limestone	above MSWB	mixed-bottom	*Liostrea sp. A*
JA29	Assameur	upper	limestone	above MSWB	mixed-bottom	*Liostrea sp. A*
JK77	Bou Kendill	lower	limestone	above FWWB	ooids	*Rhactorhynchia*
JK4	Bou Kendill	middle	marly limestone	below MSWB	soft-bottom	*Rugitella*
JK5	Bou Kendill	middle	marly limestone	below MSWB	mixed-bottom	*Zeilleria subbuculenta*
JK5.2	Bou Kendill	middle	limestone	above MSWB	mixed-bottom	*Zeilleria subbuculenta*
JK5.5	Bou Kendill	middle	marly limestone	below MSWB	mixed-bottom	*Zeilleria subbuculenta*
JK5.6	Bou Kendill	middle	limestone	below MSWB	mixed-bottom	*Zeilleria subbuculenta*
JK8	Bou Kendill	middle	marly limestone	below MSWB	soft-bottom	*Mactromya*
JK9.2	Bou Kendill	middle	marly limestone	below MSWB	soft-bottom	*Protocardia*
JK15	Bou Kendill	middle	limestone	below MSWB	mixed-bottom	*Zeilleria subbuculenta*
JK20.4	Bou Kendill	middle	marly limestone	below MSWB	soft-bottom	*Tubithyris chouberti*
JK24.9	Bou Kendill	upper	limestone	above MSWB	mixed-bottom	*Rugitella*
JK32	Bou Kendill	upper	limestone	above MSWB	soft-bottom	*Rugitella*
JK33	Bou Kendill	upper	limestone	above NSWB	soft-bottom	*Rugitella*
KF1-1	Kasba Flilo	upper	marly limestone	above MSWB	mixed-bottom	*Tubithyris chouberti*
KF1-2	Kasba Flilo	upper	marly limestone	above MSWB	mixed-bottom	*Tubithyris chouberti*
KF1-3	Kasba Flilo	upper	marly limestone	above MSWB	mixed-bottom	*Stiphrothyris*
KF1	Kasba Flilo	middle	marly limestone	below MSWB	soft-bottom	*Cingentolium*
KF2	Kasba Flilo	middle	marly limestone	below MSWB	soft-bottom	*Cingentolium*
KF2.8	Kasba Flilo	middle	marly limestone	above MSWB	soft-bottom	*Liostrea-Rhactorhynchia*
KF3	Kasba Flilo	middle	limestone	above NSWB	mixed-bottom	*Liostrea-Rhactorhynchia*
KF3.2	Kasba Flilo	middle	marly limestone	below MSWB	soft-bottom	*Nicaniella*
KF3.4	Kasba Flilo	middle	marly limestone	below MSWB	soft-bottom	*Nicaniella*
KF4	Kasba Flilo	middle	marly limestone	above NSWB	soft-bottom	*Liostrea-Rhactorhynchia*
KF4.5	Kasba Flilo	middle	marly limestone	below MSWB	soft-bottom	*Entolium*
KF5	Kasba Flilo	middle	limestone	above MSWB	mixed-bottom	*Liostrea-Rhactorhynchia*
KF5.11	Kasba Flilo	middle	marly limestone	above MSWB	soft-bottom	*Liostrea-Rhactorhynchia*
KF6	Kasba Flilo	middle	limestone	above MSWB	soft-bottom	*Rhactorhynchia*
KF7	Kasba Flilo	middle	limestone	above MSWB	mixed-bottom	*Liostrea-Rhactorhynchia*
KF17.2	Kasba Flilo	middle	marly limestone	above NSWB	mixed-bottom	*Rugitella*
KF18.2	Kasba Flilo	middle	limestone	above NSWB	mixed-bottom	*Liostrea sandalina*
TT1	Talghemt	middle	marly limestone	above MSWB	soft-bottom	*Entolium*

Supplement 3 – Stratigraphic and environmental assignments of samples.

Sample	Section	Member	Carbonate-siliciclastics	Wave-base level	Substrate	Sample group
TT1.3	Talghemt	middle	marly limestone	above MSWB	soft-bottom	*Liostrea sandalina*
TT2	Talghemt	middle	marly limestone	above MSWB	soft-bottom	*Entolium*
TT3	Talghemt	middle	marly limestone	above MSWB	mixed-bottom	*Liostrea sandalina*
TT3.5	Talghemt	middle	limestone	above NSWB	mixed-bottom	*Stiphrothyris*
TT3.7	Talghemt	middle	limestone	above NSWB	mixed-bottom	*Stiphrothyris*
TT3.9	Talghemt	middle	marly limestone	below MSWB	soft-bottom	*Entolium*
TT4	Talghemt	middle	marly limestone	above MSWB	mixed-bottom	*Entolium*
TT7	Talghemt	middle	limestone	above NSWB	soft-bottom	*Stiphrothyris*
TT8	Talghemt	middle	marly limestone	above NSWB	mixed-bottom	*Liostrea-Rhactorhynchia*
TT11	Talghemt	upper	limestone	above NSWB	mixed-bottom	*Zeilleria-Kallirhynchia*
TT14	Talghemt	upper	limestone	above NSWB	mixed-bottom	*Zeilleria-Kallirhynchia*
BT1	Tidrit	lower	marly limestone	above MSWB	mixed-bottom	*Modiolus-Rhactorhynchia*
BT1.2	Tidrit	lower	marly limestone	above MSWB	soft-bottom	*Modiolus-Rhactorhynchia*
BT1.3	Tidrit	lower	marly limestone	above MSWB	mixed-bottom	*Rhactorhynchia*
BT1.4	Tidrit	lower	marl	above MSWB	soft-bottom	*Nicaniella*
BT4	Tidrit	lower	marly limestone	above MSWB	soft-bottom	*Liostrea sandalina*
BT07	Tidrit	lower	marly limestone	above NSWB	mixed-bottom	*Liostrea sandalina*
BT09b	Tidrit	lower	marly limestone	above NSWB	mixed-bottom	*Zeilleria subbuculenta*
BT10-1	Tidrit	lower	marly limestone	above NSWB	mixed-bottom	*Liostrea sandalina*
BT10-2	Tidrit	lower	marl	above MSWB	soft-bottom	*Nicaniella*
BT14	Tidrit	lower	marly limestone	above NSWB	mixed-bottom	*Liostrea sandalina*
BT19.2	Tidrit	lower	marly limestone	above NSWB	mixed-bottom	*Liostrea sandalina*
BT25.2	Tidrit	middle	marly limestone	above NSWB	soft-bottom	*Liostrea sandalina*
BT37.2	Tidrit	middle	marly limestone	above MSWB	soft-bottom	*Liostrea sandalina*
BT38.5	Tidrit	middle	marl	below MSWB	soft-bottom	*Mactromya*
BT39.4	Tidrit	middle	marly limestone	above MSWB	mixed-bottom	*Liostrea sandalina*
BT40.6	Tidrit	middle	marly limestone	above MSWB	mixed-bottom	*Liostrea sandalina*
BT48.2	Tidrit	middle	marly limestone	above MSWB	soft-bottom	*Rostroperna*
BT50	Tidrit	middle	limestone	above MSWB	soft-bottom	*Rhactorhynchia*
BT50.6	Tidrit	middle	limestone	above NSWB	mixed-bottom	*Rhactorhynchia*
BT51.3	Tidrit	middle	marly limestone	above MSWB	soft-bottom	*Nicaniella*
BT51.4	Tidrit	middle	marly limestone	above MSWB	soft-bottom	*Nicaniella*
BT53	Tidrit	middle	limestone	above NSWB	mixed-bottom	*Liostrea sandalina*
BT53.2	Tidrit	middle	limestone	above NSWB	mixed-bottom	*Stiphrothyris*
BT53.8	Tidrit	middle	limestone	above NSWB	mixed-bottom	*Stiphrothyris*
BT54.4	Tidrit	middle	marly limestone	above MSWB	mixed-bottom	*Liostrea sandalina*
BT54.5	Tidrit	middle	marly limestone	above MSWB	mixed-bottom	*Liostrea sandalina*
BT54.6	Tidrit	middle	marly limestone	above MSWB	mixed-bottom	*Liostrea sandalina*
BT56	Tidrit	middle	marl	above MSWB	soft-bottom	*Modiolus-Rhactorhynchia*
BT56.3	Tidrit	middle	marly limestone	above MSWB	soft-bottom	*Modiolus-Rhactorhynchia*
BT57	Tidrit	middle	marly limestone	above MSWB	mixed-bottom	*Modiolus-Rhactorhynchia*
BT59.2	Tidrit	middle	marly limestone	above MSWB	mixed-bottom	*Rostroperna*
BT61	Tidrit	middle	marl	above MSWB	soft-bottom	*Nicaniella*
BT64.5	Tidrit	middle	marl	above MSWB	soft-bottom	*Nicaniella*
BT67.8	Tidrit	middle	marly limestone	above MSWB	mixed-bottom	*Rhactorhynchia*
BT67.12	Tidrit	upper	marly limestone	above NSWB	mixed-bottom	*Rhactorhynchia*
BT77	Tidrit	upper	limestone	above FWWB	ooids	*Rhactorhynchia*
BT79.2	Tidrit	upper	limestone	above NSWB	ooids	*Zeilleria subbuculenta*
BT81.2	Tidrit	upper	limestone	above FWWB	ooids	*Rhactorhynchia*
BT81.4	Tidrit	upper	limestone	above FWWB	ooids	*Rhactorhynchia*
BT87.6	Tidrit	upper	limestone	above NSWB	ooids	*Rhactorhynchia*
BT90.3	Tidrit	upper	limestone	above FWWB	ooids	*Stiphrothyris*
BT103	Tidrit	upper	limestone	above FWWB	ooids	*Stiphrothyris*
BT107	Tidrit	upper	limestone	above NSWB	mixed-bottom	*Stiphrothyris*
BT109	Tidrit	upper	limestone	above FWWB	ooids	*Zeilleria subbuculenta*

Supplement 3 (cont.) - Stratigraphic and environmental assignments of samples.

10. Ecology of brachiopods and bivalves in the Upper Jurassic sponge communities of southern Germany

(with Franz T. Fürsich)

Abstract. Level-bottom benthic communities that inhabited deep-shelf sponge habitats in southern Germany during the Late Jurassic were characterized by a distinctive guild structure with high dominance of pedunculate brachiopods. Variations in siliciclastic supply and substrate consistency had invariably significant effects on abundances of brachiopod and bivalve species. Abundances of guilds correlate with variations in siliciclastic supply in the *Sutneria platynota* Zone only, and with variations in substrate consistency in the *Subnebrodites planula*, *Ataxioceras hypselocyclum-Crussoliceras divisum*, and *Hybonoticeras beckeri* zones. During the Oxfordian and Early Kimmeridgian, the large-sized terebratulids *Placothyris* and *Loboidothyris* and the rhynchonellid *Lacunosella* inhabited hard-bottom habitats represented by sponge biostromes and sponge-microbial mounds. The small-sized brachiopods *Zittelina, Monticlarella* and *Aulacothyris* and the epibyssate bivalve *Aulacomyella* were abundant on soft bottoms. Shallow burrowing deposit-feeding bivalves locally occur in shell-poor deposits representing soft-bottom conditions, but their numerical abundance is invariably very low. During the Late Kimmeridgian, environments were more differentiated owing to a relative sea level fall. Shallower environments dominated by the brachiopods *Juralina* and *Torquirhynchia* and deeper environments by the brachiopod *Loboidothyris*. In the *Ataxioceras hypselocyclum* Zone, horizontal community replacements between sponge-rich, hard-bottom habitats with large-sized brachiopods, and mud-rich habitats with small-sized brachiopods, *Aulacomyella* and *Chondrites* on the scale of several decimeters constrain the effects of varying terrigenous supply and wave base levels. They thus imply that (1) variations in substrate consistency governed species and guild abundances, and (2) sponge communities dominated by brachiopods might be temporally living under oxygen-deficient conditions because co-eval soft-bottom habitats were characterized by dysaerobic faunas. Rarity of shallow burrowing suspension-feeding bivalves in sponge habitats might by related to high substrate consistency, but their similarly low abundance in soft-bottom habitats indicates that factors related to low flow velocity or low oxygen concentrations in deep-shelf habitats may limit their distribution. Higher abundance of brachiopods than of bivalves in deep-shelf habitats is in accord with the hypothesis that brachiopods possessed more efficient feeding strategy under limited flow velocities than bivalves with higher pumping rates, and that their dominance was possibly enhanced by reduced competition for space in such flow-limited habitats.

Introduction

Sponge-dominated benthic communities inhabited extensive areas on the northern shelf of the Tethys ocean during the Late Jurassic (Leinfelder, 2001). They were commonly occupied by relatively diverse and numerically abundant brachiopods that locally occur in nests or lensoid concentrations in sponge or sponge-microbial biostromes and mounds (Brugger, 1999; Reolid, 2005). Similar sponge-dominated communities with brachiopods were analyzed in the Sinemurian deposits of the Central High Atlas (Chapter 7). In that study, it was proposed that abundance of brachiopods and concomitant rarity of epifaunal bivalves in deep-shelf, hard-bottom environments can be explained by combined effects of restricted flow velocity that is commonly coupled with oxygen-poor conditions, leading to (1) reduced feeding efficiency of epifaunal bivalves because of their high pumping rates, and (2) reduced grazing and reduced competition intensity for space owing to lower abundance of organisms with high metabolic requirements. In this chapter, benthic communities that occupied deep-shelf, sponge-rich habitats of southern Germany (fig. 1) during the Oxfordian and Kimmeridgian are described and analyzed. It is evaluated whether brachiopod dominance in Late Jurassic sponge-dominated environments is similarly related to low flow velocity and/or reduced oxygen concentrations that (1) produced feeding and physiological constraints that were more limiting for epifaunal bivalves than for brachiopods, and (2) reduced intensity of grazing and competition for space in hard-bottom habitats, as was suggested for the Sinemurian sponge communities of the Central High Atlas.

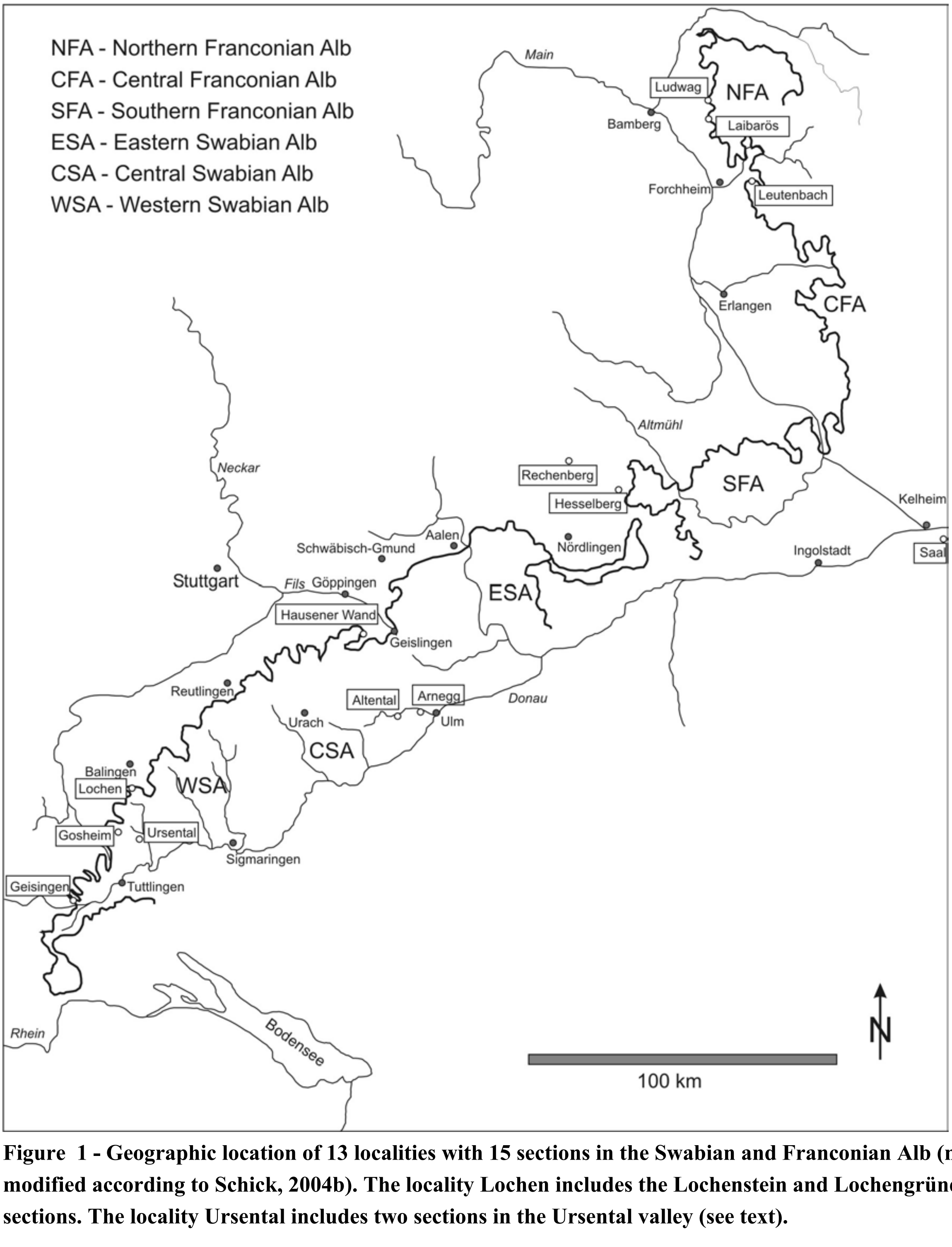


Figure 1 - Geographic location of 13 localities with 15 sections in the Swabian and Franconian Alb (map modified according to Schick, 2004b). The locality Lochen includes the Lochenstein and Lochengründle sections. The locality Ursental includes two sections in the Ursental valley (see text).

Setting

The depositional area of southern Germany was situated on the northern shelf of the Tethys ocean during the Late Jurassic (Meyer and Schmidt-Kaler, 1989). It formed an epicontinental sea bordered in the northern part by the London-Brabant and Rhenish landmasses and in the eastern part by the Bohemian Land. It was connected with Boreal realm via the Hessian Seaway that was closed in the latest Jurassic. In general, this sea was subdivided into the Franconian – South Bavarian Platform in the eastern part that passed into the Swabian Basin towards the west. The Swabian Basin was rimmed in the western part by the Swabian reef area (Meyer and Schmidt-Kaler, 1990). Further to the west, the Swabian reef area graded into the Swiss Jura carbonate platform. To the south, it was replaced by pelagic facies of the Tethys ocean.

The Upper Jurassic succession in southern Germany is about 400-600 m thick and starts with condensed glauconitic sandy marls that belong to the Lower Oxfordian *Cardioceras cordatum* Zone (Fig. 2). Sponge biostromes appear in the upper part of the *Gregoryceras transversarium* Zone. The Middle Oxfordian-Kimmeridgian succession consists of large-scale alternation of marl-rich and carbonate-rich intervals. It begins with the marl-rich Upper Oxfordian deposits, followed by the carbonate-rich *Subnebrodites planula* Zone, the marl-rich *Sutneria platynota-Ataxioceras hypselocyclum-Crussoliceras divisum* zones, and the carbonate-rich Upper Kimmeridgian zones, with marl-rich deposits of the Zementmergel and Mergelstetten formations in the uppermost parts of the Kimmeridgian (Schmid et atl., 2005). Variations in marl and limestone abundance probably reflect combined effects of varying siliciclastic input from the north (Rhenish Land) and varying export of carbonate mud from the Swiss Jura platform (Pittet et al., 2000; Bartolini et al., 2003). In terms of horizontal facies changes, well-bedded limestones and marls may laterally pass into sponge biostromes and massive bioherms with sponges and microbial crusts (Roll, 1934; Fritz, 1958; Aldinger, 1961; Wagenplast, 1972; Flügel and Steiger, 1981; Lang, 1989; Selg and Wagenplast, 1990; Schmid, 1996). Abundance of sponge reefs fluctuated in time and attained the peak early in the Late Kimmeridgian (Schmid et al., 2005). During the Oxfordian and Early Kimmeridgian, sponge reefs were formed predominantly in low-energy habitats below maximum storm wave base. In contrast, sponge reefs probably reached to shallower habitats during the Late Kimmeridgian because they are associated with storm-reworked beds and well sorted carbonate sands (Koch et al., 1994; Pawellek and Aigner, 2003).

Methods

15 sections with the Oxfordian-Kimmeridgian deposits were samples in the Swabian and Franconian Alb of southern Germany (Fig. 1). The absolute abundance of brachiopod and bivalve individuals was estimated with the maximum number of individuals (XNI) approach (i.e., each valve and shell was counted as one individual). 94 samples with a minimum sample-level number of 25 individuals were analysed. Brachiopods were determined by A.T. and bivalves by F.T.F. to species level. Discrimination of groups of samples with similar abundances was performed on species level. Non-metric multidimensional scaling (NMDS) analyses were based on species and guild abundances. R-mode based one-way analysis of similarities (ANOSIM) tested whether there are any differences in abundance patterns among brachiopods, protobranchs, filibranchs, pseudolamellibranchs, and

eulamellibranchs. Q-mode based one-way ANOSIM was used to test differences in community composition between habitats differing in (1) siliciclastic/carbonate supply (i.e., marls, marly limestones, and limestones), (2) substrate consistency (i.e., mudstones and wackestones with tuberoids were assigned to mixed-bottom habitats, and boundstones to hard-bottom habitats), and (3) wave-base level. Well-sorted grainstones/rudstones were assigned to habitats above fair-weather wave base (FWWB), amalgamated bioclastic packstones to habitats above normal storm wave base (NSWB), and floatstones, wackestones and mudstones, locally with thin, tuberoid-rich interbeds, to habitats below NSWB. Owing to substantial between-zone stratigraphic differences, one-way ANOSIM testing environmental effects on community composition is evaluated separately for the Oxfordian (1) *Dichotomoceras bifurcatus* and *Epipeltoceras bimammatum* zones, the Lower Kimmeridgian (2) *Subnebrodites planula* Zone, (4) *Sutneria platynota* Zone, (5) *Ataxioceras hypselocyclum* and *Crussoliceras divisum* zones, and (6) the Upper Kimmeridgian *Hybonoticeras beckeri* Zone. Samples from the *Aulacostephanus mutabilis* Zone were not evaluated with ANOSIM because they are derived from one section with relatively uniform deposit types. The Oxfordian-Lower Kimmeridgian samples were invariably assigned to habitats below normal storm wave base. The effects of varying wave-base level were thus evaluated for the Upper Kimmeridgian samples only.

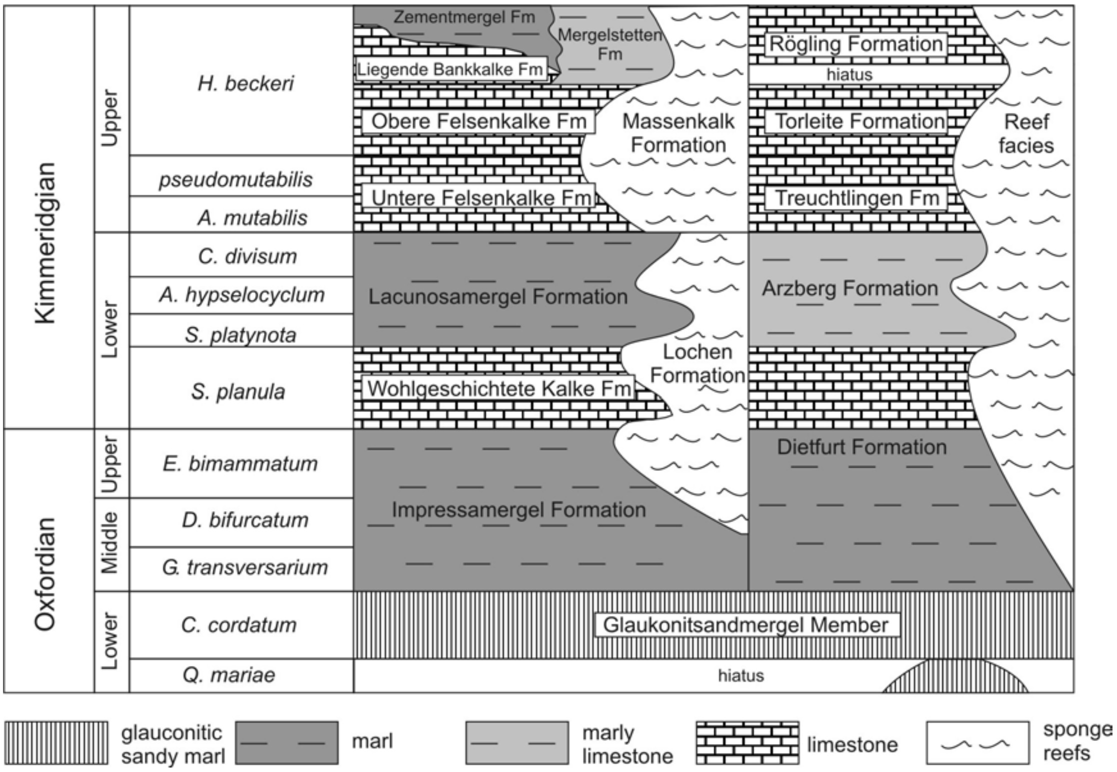


Figure 2 - Oxfordian-Kimmeridgian lithostratigraphic formations of southern Germany (modified according to Schmid et al., 2005).

Sections

Oxfordian

Lochengründle. An about 8 meters thick succession through the *Dichotomoceras bifurcatus* Zone (Middle Oxfordian) forms a small road outcrop about 250 m southeast of the Lochenstein hill, near the road from Tieringen to Balingen in the Swabian Alb (Roll, 1934; Schädel, 1957; Matyszkiewicz, 1997). The section exposes meter-scale sponge-microbial mounds that alternate and laterally pass into marl-limestone bedsets rich in tuberoids, sponges, ammonites, and small brachiopods and bivalves (Fig. 3). It represents a transition between the basinal Impressamergel Formation and the mound-rich Lochen Formation. Tuberoids in marls are locally accumulated in thin, mm-scale, well sorted and densely packed layers.

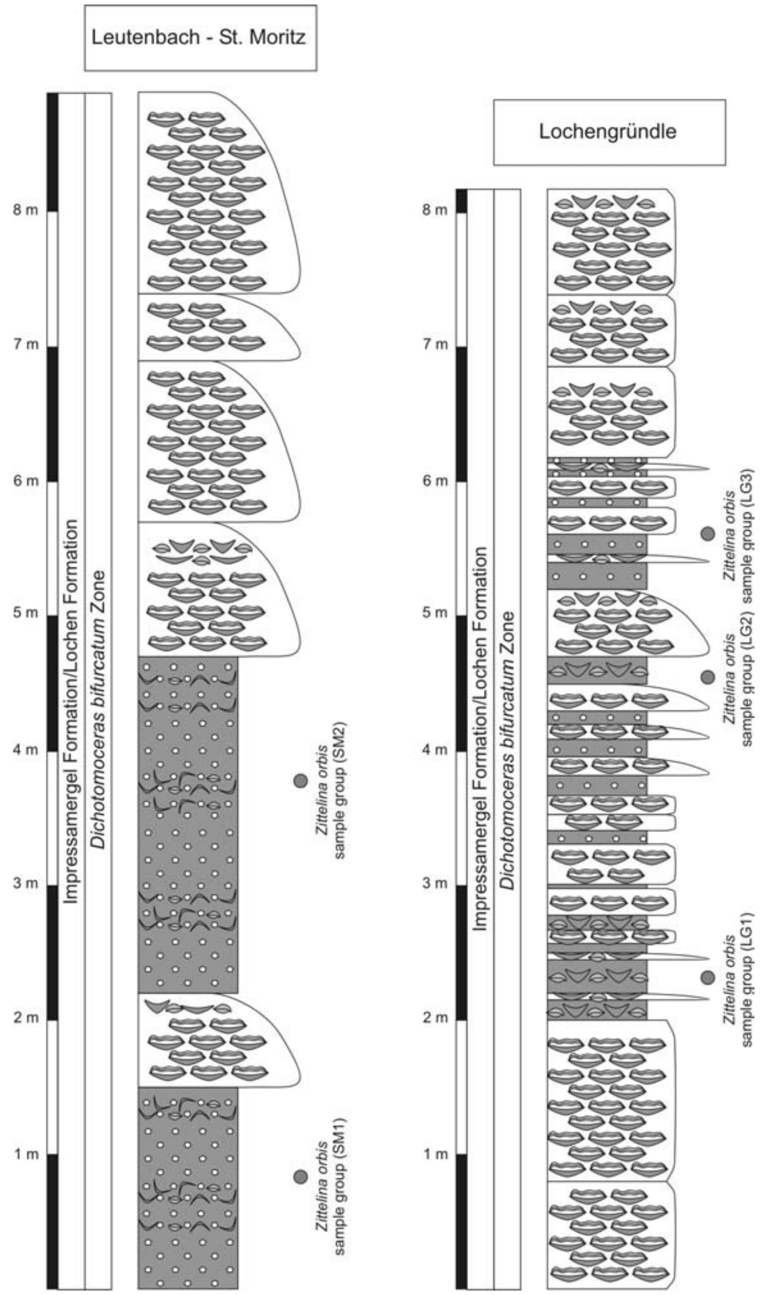


Figure 3 - Stratigraphic distribution of sample groups in the two Middle Oxfordian sections of the *Dichotomoceras bifurcatus* Zone. Explanations: Fig. 9.

Leutenbach. Road outcrops are situated about 1 km east of the Leutenbach village near the St. Moritz Kapelle, near the road from Leutenbach to Hundsboden, 9 km east of Forchheim in the Northern Franconian Alb (Fig. 3). They expose an about 9 meters thick succession of tuberoid-rich marls that alternate with 1 to 1.5-m thick sponge-microbial mounds (Richter, 2000). Two samples belonging to the *Dichotomoceras bifurcatus* Zone were collected here (Middle Oxfordian).

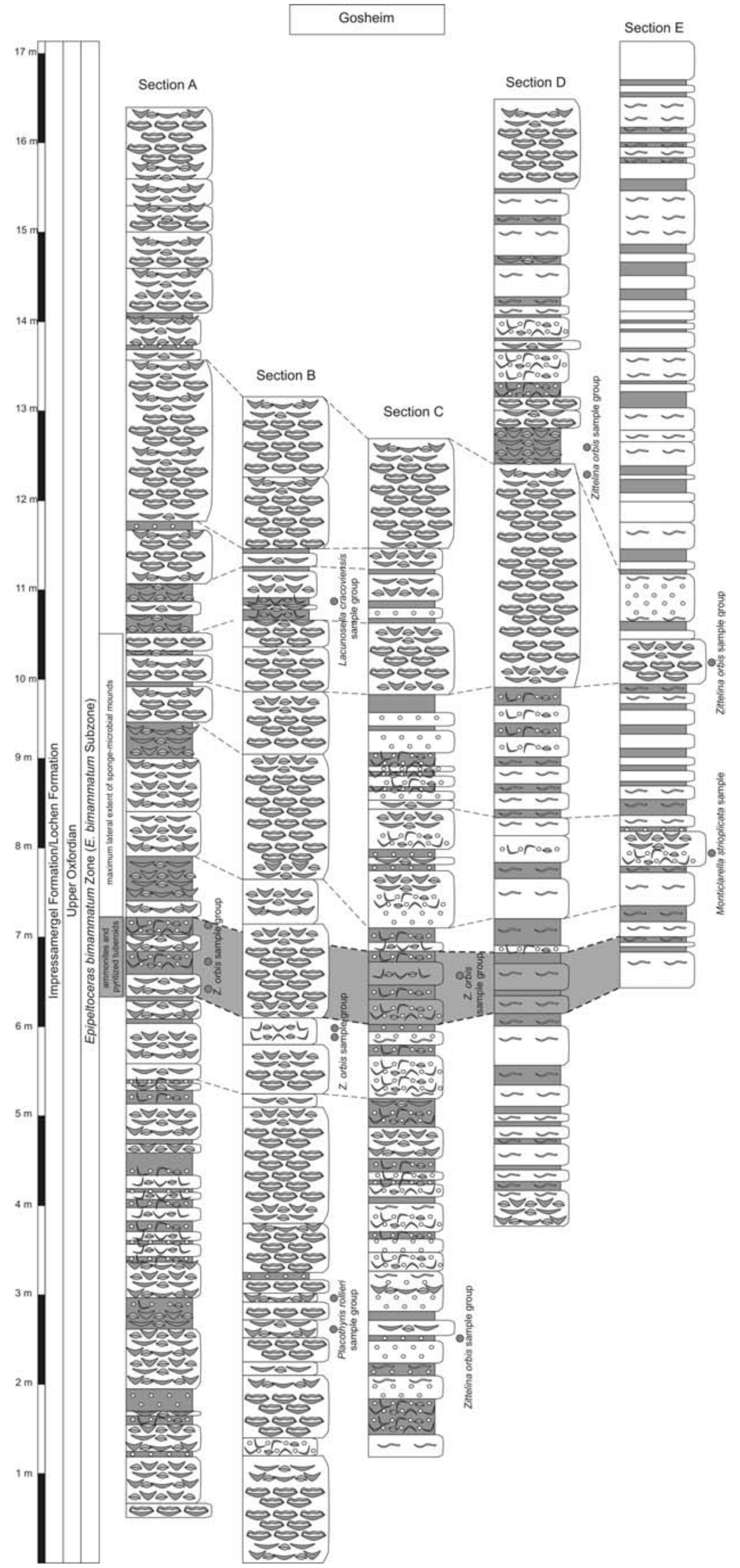


Figure 4 – Lateral replacements between soft-bottom, Chondrites-rich deposits and sponge mounds in the Gosheim section (*Epipeltoceras bimammatum* Zone, Upper Oxfordian). In the middle part, glauconitic-rich intervals with ammonites marks a base of the maximum lateral extent of sponge mounds. The distance between the two marginal sections A and E is about 100 m. Explanations: Fig. 9.

Gosheim. An old quarry is situated near the southeastern margin of Gosheim, near the road from Gosheim to Böttingen in the Swabian Alb. It exposes an about 200 meters long complex of meter-scale sponge-microbial mounds that vertically and laterally alternate with mud-rich and tuberoid-rich marls and limestones (Schmid et al., 2001; Leinfelder, 2001). They thus show a replacement of mounds and biostromes by level-bottom deposits of the Impressamergel Formation (Fig. 4). A 20-m thick succession in the lower part of the section with abundant sponge-microbial mounds and mixed, siliciclastic-carbonate deposits belongs to the *Epipeltoceras bimammatum* Zone. The upper, 20-m thick part of the section above the boundary between the *E. bimammatum* and *Subnebrodites planula z*ones is characterized by a substantial decrease in extent and thickness of sponge-microbial mounds and by a dominance of shell-poor limestones. Comparable sponge-microbial mounds of the *Epipeltoceras bimammatum* Zone were described from the Plettenberg section by Olivier et al. (2004) and Ruf et al. (2005a). A 1-m thick, marl-limestone bedset rich in glauconite, ammonite shells and macrobenthic fauna is present about 6-7 meters above the base of the section. This interval marks the maximum lateral extension of the mound complex in the Gosheim section (Schmid et al., 2001). Another interval rich in glauconite, ammonites and brachiopods is present 6 meters higher in the succession. Bedded marl-limestone couplets that laterally replace mounds are characterized by abundance of *Chondrites*.

Lower Kimmeridgian

Lochenstein. Natural outcrops that are exposed near the path from the Lochengründle section to the Lochenstein hill. About 7.5 meters of poorly bedded sponge-microbial mounds alternate with beds rich in sponge debris and tuberoids (Fig. 5). They belong to the *Subnebrodites planula* Zone (Lower Kimmeridgian, Schädel, 1957). Similar deposists of comparable age located about 500 meters to the southwest near the Lochen youth hostel were described by Matyszkiewicz (1997).

Hesselberg. A small abandoned quarry is situated on the Hesselberg hill, 2 km NE of Gerolfingen near Dinkelsbühl in the Southern Franconian Alb (Fig. 5). An about 8.5 meters thick succession of sponge-microbialite mounds and marly tuberoid-rich limestones with sponges and brachiopods belongs to the upper parts of the Dietfurt Formation (*S. planula* Zone, Schmidt-Kaler, 1991). The *S. planula* Zone is higher replaced by marls rich in sponges and ammonites of the *S. platynota* Zone.

Rechenberg. An old abandoned quarry on the Rechenberg hill, 2 km NW of Heidenheim exposes an about 5.5 meters thick limestone-rich succession of sponge-microbial mounds and tuberoid-rich marly limestones and limestones with common ammonites (Fig. 5, Schmidt-Kaler, 1991). They belong to the *S. planula* Zone (Dietfurt Formation).

Ludwag. An abandoned quarry is situated about 800 meters NNW of Ludwag in the Northern Franconian Alb. It belongs to the so-called Würgau-Görau reef tract that passed to the south into the Ludwag Bay. An about 50 meters thick succession of the Lower Kimmeridgian (Brachert, 1986, 1992) is formed in the lower part by the limestone-dominated, sponge-rich *S. planula* Zone (ca. 10 m) that belongs to the Dietfurt Formation. Higher, the Arzberg Formation consists of about 6 m-thick, marl-rich *S. platynota* Zone with sponge biostromes (Fig. 6), the limestone-rich *A. hypselocyclum* Zone with sponge-microbial mounds and tuberoid limestones (ca. 16 m), and the *C. divisum* Zone with marl-rich intervals in the lower part, and abundant debris flows in the upper part (ca. 16 m).

Laibarös. An about 3.5 m thick section through the lowermost parts of the Arzberg Formation is represented by natural outcrops ca. 750 m SW of the Laibarös village in the Northern Franconian

Alb (Fig. 6). Sponge-rich marls and marly limestones alternate with dm-scale sponge-microbial mounds and belong to the *S. platynota* Zone (Brugger, 1999). Six samples were collected in sponge-rich marly limestones. Three samples represent replicates from one bed that were collected in about 2-m long intervals (LA3-1, 2, 3) and one sample was derived from a small sponge-microbial mound (Sample LA4).

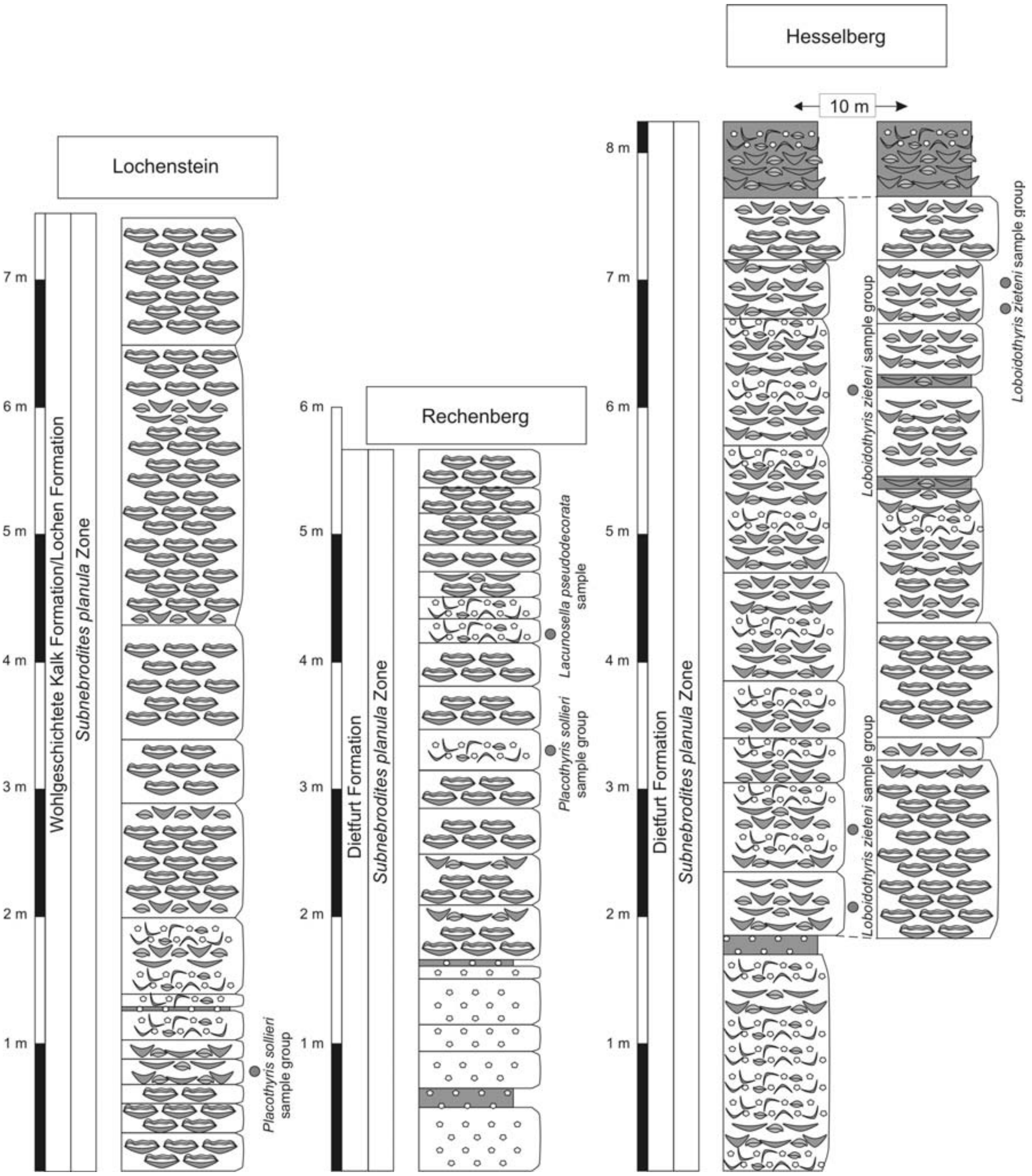


Figure 5 - Stratigraphic distribution of sample groups in three sections of the *Subnebrodites planula* Zone (Lowermost Kimmeridgian). Explanations: Fig. 9.

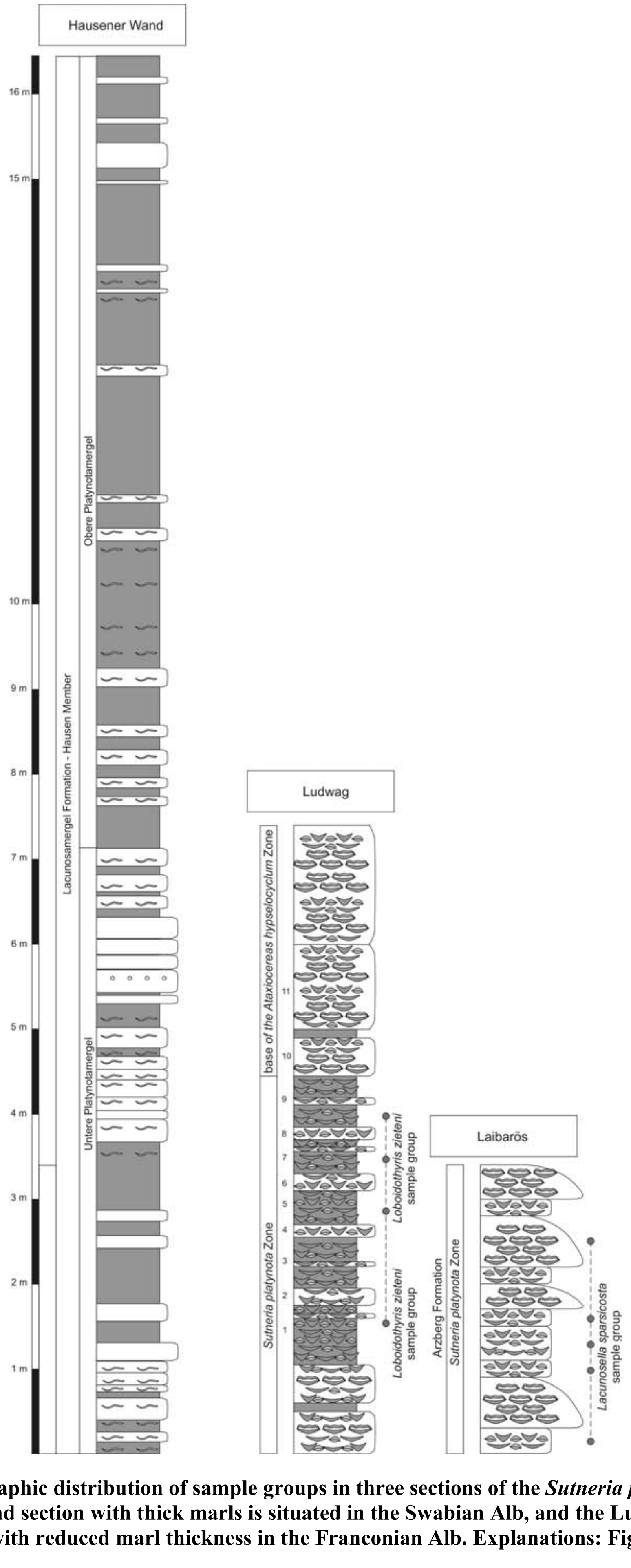


Figure 6 - Stratigraphic distribution of sample groups in three sections of the *Sutneria platynota* Zone. The Hausener Wand section with thick marls is situated in the Swabian Alb, and the Ludwag and Laibarös sections with reduced marl thickness in the Franconian Alb. Explanations: Fig. 9.

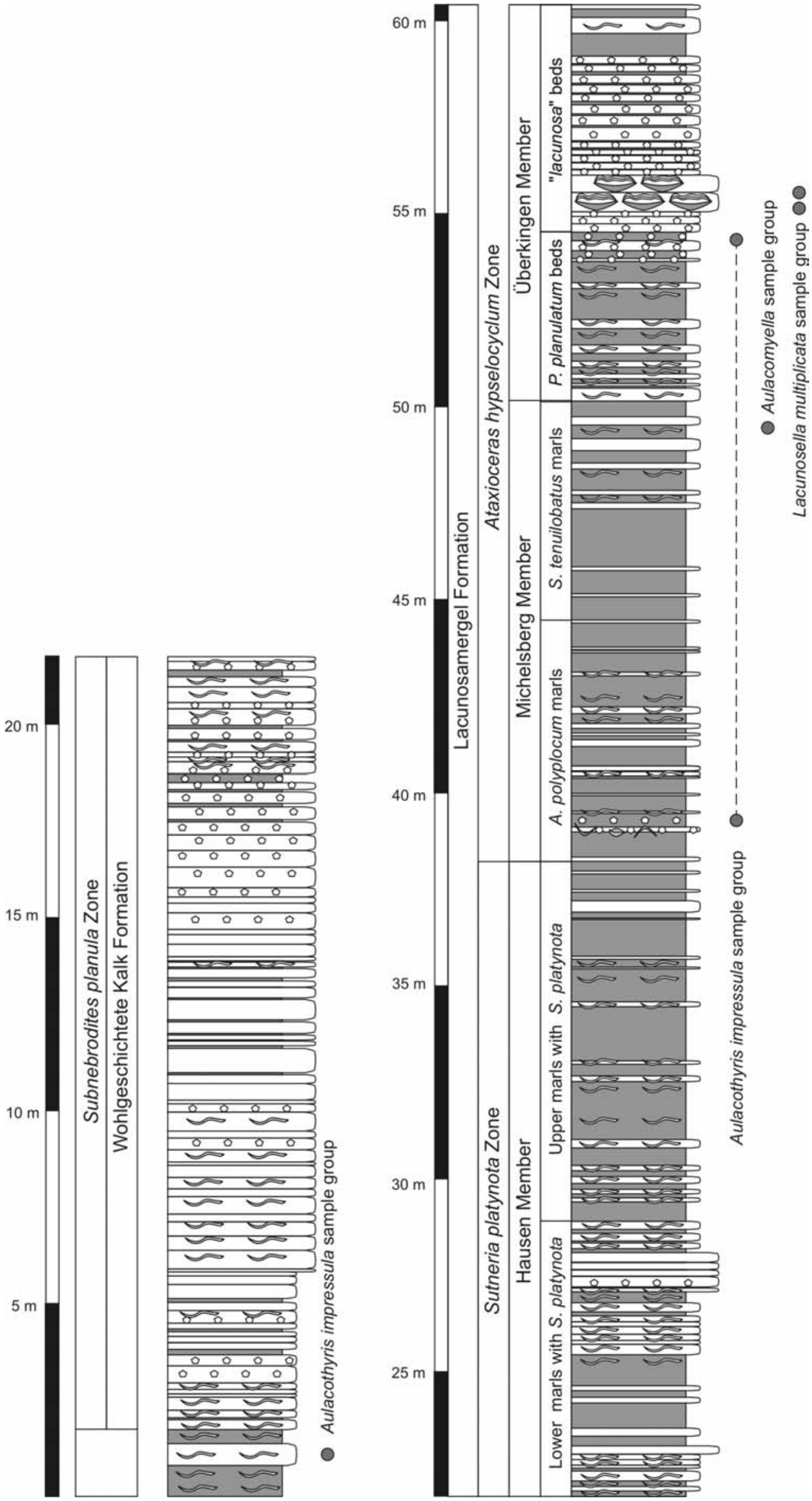


Figure 7 - The Hausener Wand section showing the Lower Kimmeridgian succession typical of the Swabian Alb. The section is subdivided into the lithostratigraphic units according to Schick (2004a). Explanations: Fig. 9.

Hausener Wand. This is a type section of the Lacunosamergel Formation (Schick, 2004). Natural outcrops are situated on the southern slope of the Michelsberg, ca. 500 m NE of Hausen an der Fils, west of Bad-Überkingen. At the base of the section (Fig. 7), bioturbated marls and marly limestones with *Chondrites* correspond to the boundary between the Impressamergel (Oxfordian) and Wohlgeschichtete Kalke formations (Lowermost Kimmeridgian). Well-bedded bioturbated mudstones with dispersed tuberoids of the Wohlgeschichtete Kalke Formation are about 20 meters thick (*S. planula* Zone). The lower part of the Lacunosemergel Formation, represented by the Hausen (*S. platynota* Zone) and Michelsberg members (lower part of the *A. hypselocyclum* Zone), is formed by an about 27 m-thick succession of bioturbated marls and mudstones that locally contain dispersed bivalves and small-sized brachiopods. Some beds are rich in ammonite fragments that are rarely encrusted by oysters. The lower part of the Überkingen Member is formed by the so-called Planulatumbänke that are 4.5 m-thick and consist of alternation of bioturbated marls with mudstones, in the upper part with abundant tuberoids and small-sized brachiopods. These beds are relatively abruptly replaced by a 5.5 m-thick carbonate-rich interval with 20-30 cm-thick limestone beds and thin marly layers (Lacunosabänke), capped by a biostratigraphic marker bed with an ammonite *Orthosphinctes (Ardescia) perayensis* (Schick, 2004b). This interval contains dm-scale sponge-microbial mounds with brachiopods that are termed as "*lacunosa*-Stotzen". This term is specifically used for sponge-microbial mounds rich in rhynchonellids that occur in the carbonate-rich interval in the upper part of the *A. hypselocyclum* Zone (Fig. 8, Malm γ3k, Geyer and Gwinner, 1979). In this stratigraphic interval, sponge-microbial mounds of the Swabian Alb contain in their marginal, basal or topmost parts abundant rhynchonellid brachiopods of the genus *Lacunosella*. In contrast, central parts of mounds are rich in microbial crusts and brachiopods are substantially less common. Sponge-microbial mounds pass on short distances to tuberoid-rich marls and marly limestones with *Chondrites* and rare benthic fauna (Fig. 9).

Geisingen. A large quarry exposing the Oxfordian-Kimmeridgian deposits is situated ca. 500 m NE of Geisingen/Donau. The lower part of the section was figured by Ruf et al. (2005b) and the upper part by Schick (2004b). These lithostratigraphic units represent the *A. hypselocyclum* and *C. divisum* zones. An about 8.5 m-thick succession belonging to the upper parts of the *A. hypselocyclum* Zone is formed by spatially variable meter-scale sponge mounds with rare and thin microbial crusts (Fig. 8). They are mainly formed by sponge marls and sponge-rich marly limestones and contain abundant rhynchonellid brachiopods and ammonites. These mounds laterally pass into marl-limestone bedsets (Fig. 10), in the lower parts with dominance of marls and in the upper parts with dominance of limestones (Lacunosabänke). They are bioturbated (*Chondrites*), mud-rich and may contain the common bivalve *Aulacomyella*. This bivalve is forming loosely to densely-packed multiple pavements in slightly bioturbated marls or marly limestones. On the top of this interval, a bed of bioturbated wackestone/floatstone with an ammonite *Orthosphinctes (Ardescia) perayensis* is present (Schick, 2004b). The base of the *C. divisum* Zone is marked by an about 1 to 1.5 meters thick bioturbated marl that locally contains loosely packed small sponges. The *C. divisum* is about 9 meters thick. The lowermost part is formed by alternation of bioturbated marls and mudstones, corresponding to the upper part of the Überkingen Member. Higher, sponge-microbial boundstones with dish-shaped sponges alternate with tuberoid-rich marls (Drackenstein Formation). The upper part of the *C. divisum Zone* is formed by marly, sponge-rich boundstones.

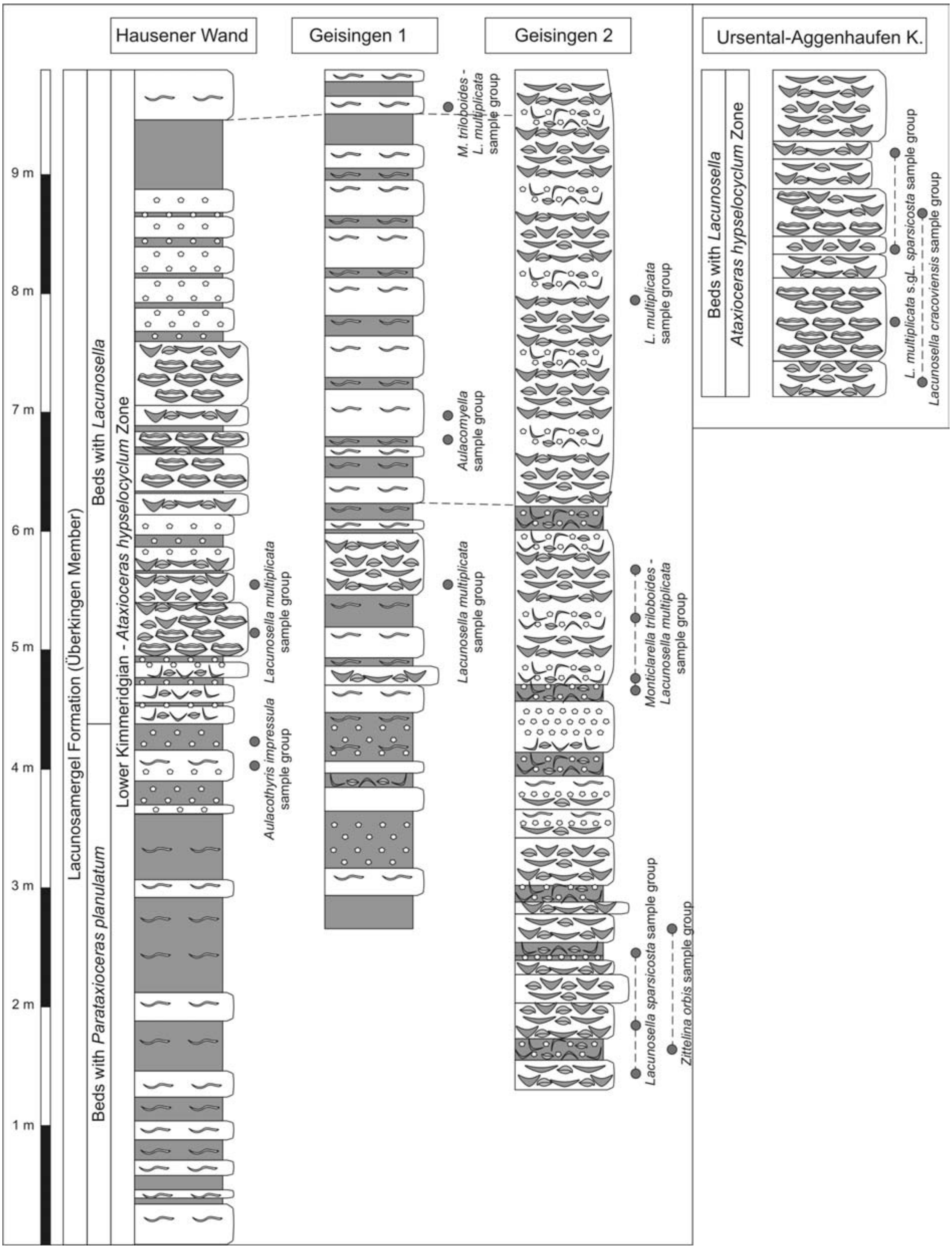


Figure 8 - Stratigraphic distribution of sample groups in the upper part of the *Ataxioceras hypselocyclum* Zone with the so-called Lacunosabänke. They contain sponge-microbial beds rich in the rhynchonellid *Lacunosella*. Explanations: Fig. 9.

Ursental-Aggenhausen Kapelle. A small outcrop near a forest pathway in the Ursental valley, ca. 3 km east of Mahlstetten, about 200 m south of the Aggenhausen Kapelle. A 3 m-thick and 10 m-long section exposes sponge-microbial boundstones. They are enriched in marly admixture and contain less common microbial crusts in the upper part (Fig. 8). About 1-2 meters long and 10-20 cm-thick lenses rich in rhynchonellid brachiopods are situated either near bedding planes or in marginal parts of mounds. In these parts, brachiopods are loosely packed and distributed in small clusters formed by 4-5 individuals. They are mostly articulated and complete, commonly coated by microbial crusts and localized in interspaces between sponges. This outcrop belongs to the *A. hypselocyclum* Zone (Schweigert, pers. comm.) and is stratigraphically equivalent to the rhynchonellid-rich Lacunosabänke (Schick, 2004a) in the Hausener Wand and Geisingen sections. This interval belongs to the Überkingen Member of the Lacunosamergel Formation (Schick, 2004a).

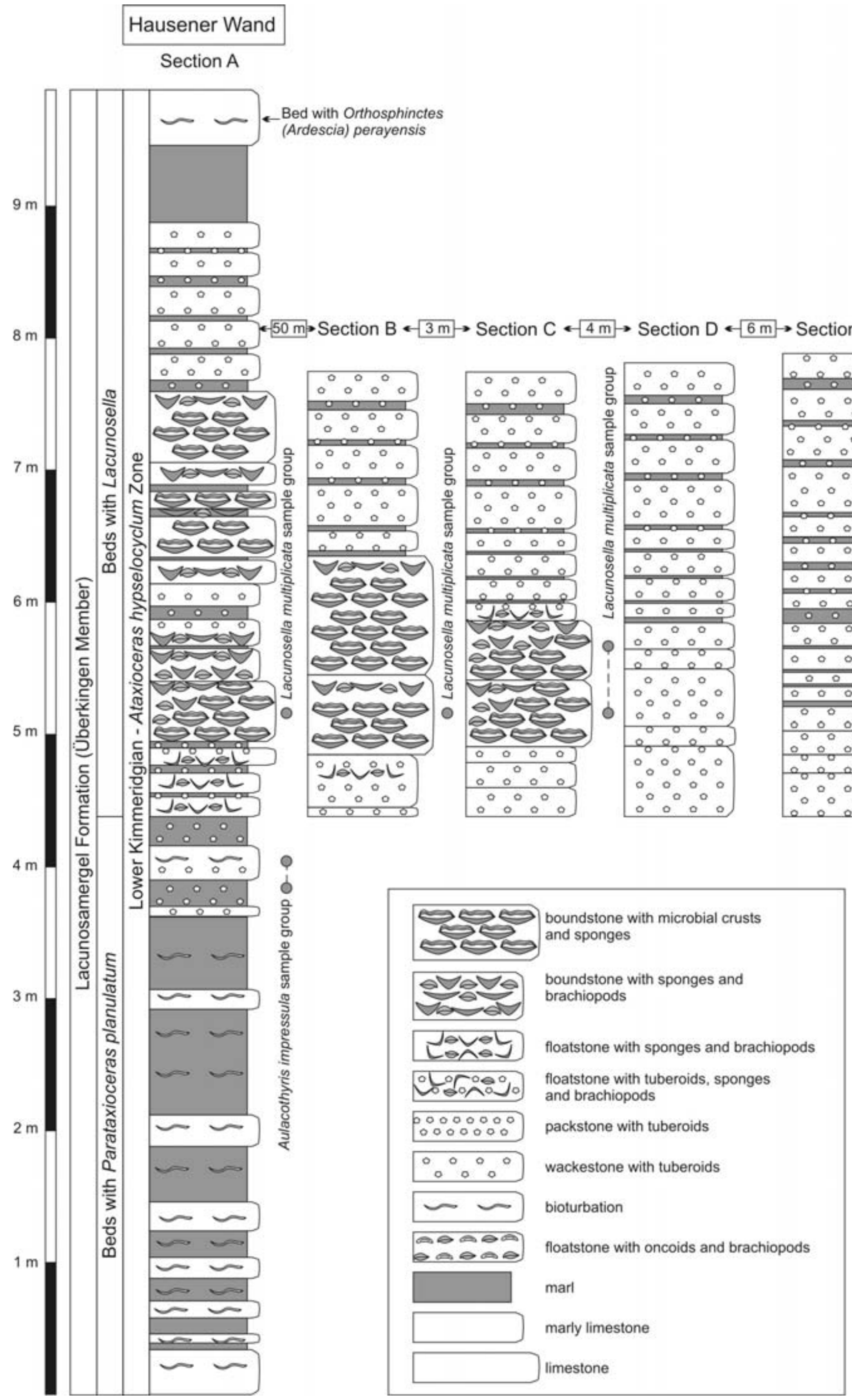


Figure 9 - Horizontal variation of the Lacunosabänke in the upper part of the *Ataxioceras hypselocyclum* Zone in the Hausener Wand section. Note small-scale replacements of sponge-thrombolitic deposits with tuberoid-rich marls.

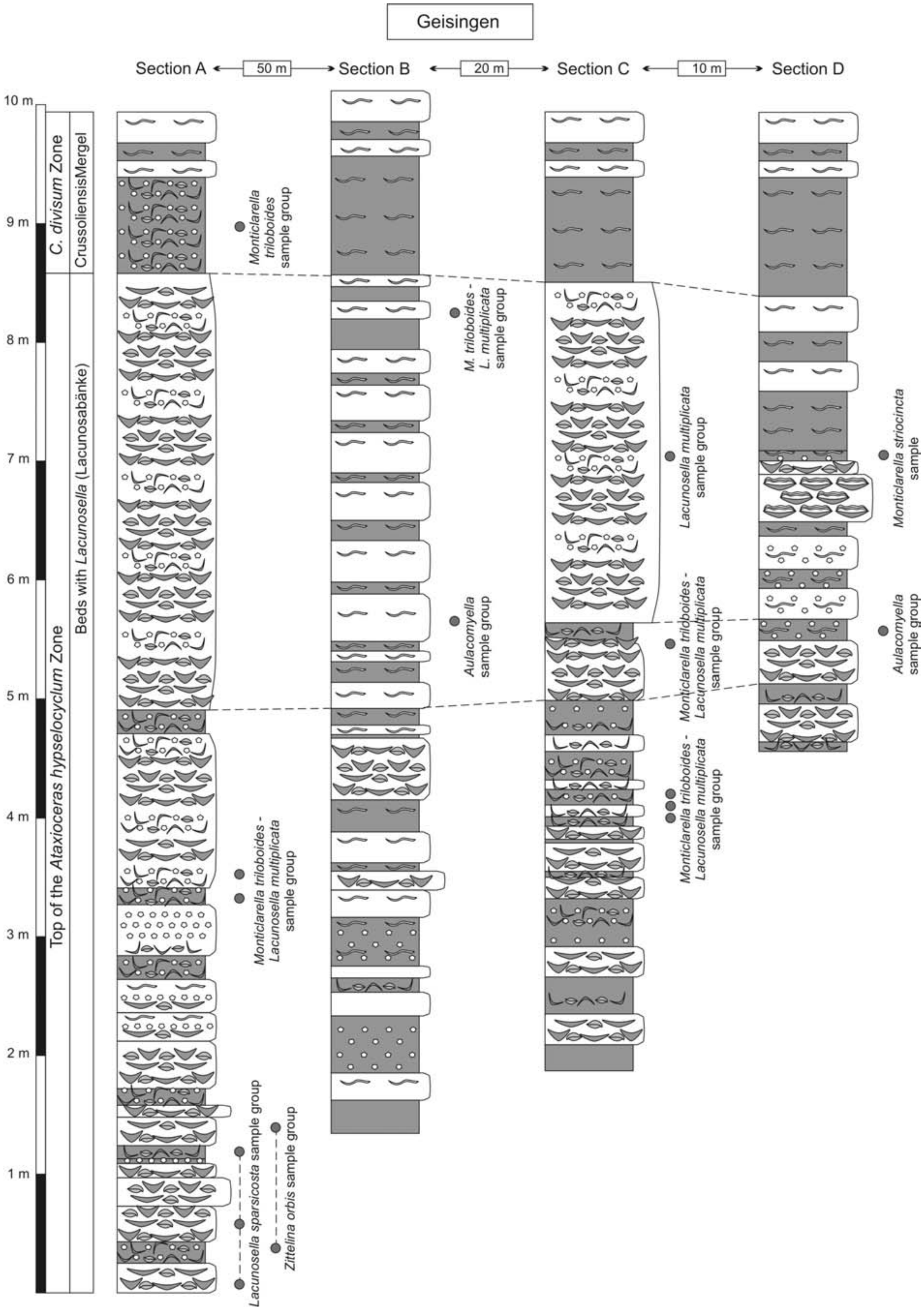


Figure 10 - Horizontal variation of the Lacunosabänke in the upper part of the *Ataxioceras hypselocyclum* Zone in the Geisingen section. Note small-scale replacements of sponge-brachiopod deposits with marls rich in the *Chondrites* burrows and the bivalve *Aulacomyella*. Explanations: Fig. 9.

Upper Kimmeridgian

Ursental-Risiberg. A small outcrop near a forest pathway in the Ursental valley in the Swabian Alb, ca. 1 km east of the Risiberg village near Spaichingen. An about 11-m thick limestone-rich succession belongs to the *Aulacostephanus mutabilis* Zone (Schweigert, pers. comm.) and can be attributed to the Untere Felsenkalke Formation. In the lower and middle part of the section, sponge-microbial mounds alternate with limestone beds rich in tuberoids and sponge fragments (Fig. 11). In the upper part, tuberoid packstones and sponge-microbial boundstones contain abundant brachiopods, locally in rock-forming concentrations. In the uppermost beds, sponges are strongly degraded, and brachiopods and sponge fragments are asymmetrically coated by microbial crusts.

Saal. A large quarry with an about 85 meters thick succession of the Upper Kimmeridgian deposits is situated ca. 1 km south of Saal and 6 km east of Kelheim. Massive sponge-microbial limestones with debris flows are present in the lower part of the quarry. In the upper parts of the quarry, framestones and rudstones with coral colonies and coral debris are locally laterally replaced by brachiopod shell beds dominated by the terebratulid *Juralina insignis* (Fig. 12, Brugger, 1999; Klug et al., 2004). These brachiopod-rich are assigned to the Upper Kimmeridgian (*Hybonoticeras beckeri* Zone, Barthel and Schairer, 1978; Schairer and Sylla, 1996). Gastropods and brachiopods were described by Schlosser (1881a, b). Bivalves were described by Boehm (1881) and revised by Yamani (1975).

Altental. A large quarry situated 3 km east of Blauberen near Ulm in the Swabian Alb exposes an about 130 meters thick succession of the Upper Kimmeridgian-Lowermost Tithonian deposits (Koch and Senowbari-Daryan, 2000). The *A. pseudomutabilis* Zone and the lower part of the *H. beckeri* Zone are represented by peloid-lithoclast-ooid deposits that are locally replaced by meter-scale sponge-microbial mounds with brachiopods. In turn, these mounds are spatially replaced by bedded marl-limestone deposits. Brachiopods were preferentially concentrated on upper mound margins that were oriented towards restricted lagoons enclosed between amalgamated sand bars (Koch et al., 1994; Koch and Senowbari-Daryan, 2000). Two samples with brachiopods and bivalves were collected in a sponge-microbial mound that corresponds to the upper part of the *H. beckeri* Zone (mound 1 on Table 1-1 in Koch and Senowbari-Daryan [2000]). Peloid-lithoclast-ooid deposits are overlain by marl-limestone alternation with black to dark grey, organic-rich marls and local sponge-microbial mounds. The Lowermost Tithonian deposits are represented by debris flows with blocks of coral and sponge-microbial mounds.

Arnegg. An abandoned quarry situated ca. 1 km SE of Arnegg near Ulm in the Swabian Alb exposes the Upper Kimmeridgian succession showing replacement of sponge-microbial deposits by coral-sponge-microbial deposits, and finally by coral reefs (Paulsen, 1964; Laternser in Leinfelder et al., 1994). Three samples were collected in the quarry A of Paulsen (1964). One sample is derived from a 2-m thick mound with sponges, coral fragments, stromatolitic crusts and high proportions of bivalve macroborings. Two samples are derived from about 50-cm thick, densely packed and well sorted bioclastic rudstones that alternate with framestones rich in platy corals. Rudstones are rich in highly fragmented and disarticulated crinoidal, mollusc, brachiopod and coral debris that is commonly concordantly oriented. Rudstones are characterized by complex stratification consisting of cm-scale layers that vary in packing, sorting and composition. These samples are assigned to the *H. beckeri* Zone.

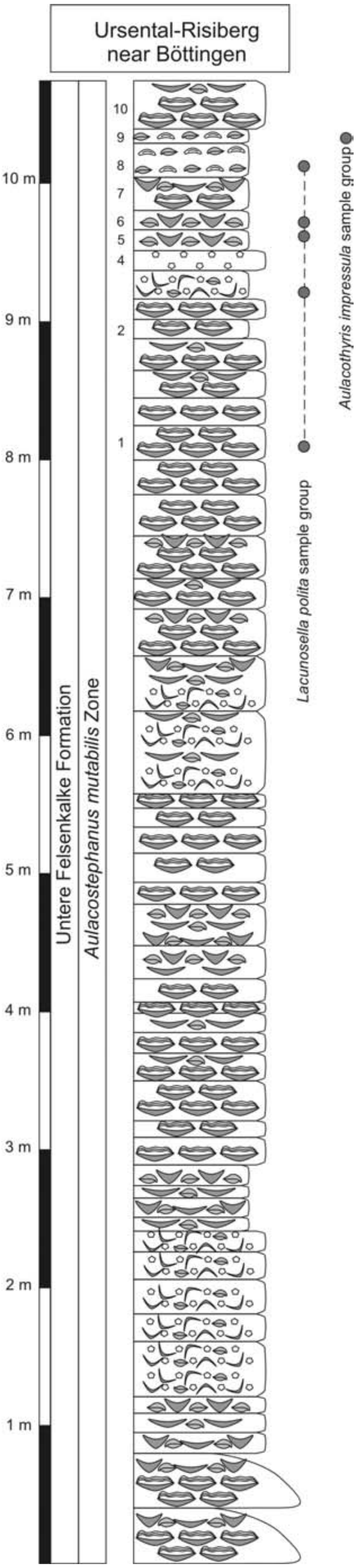


Figure 11 - Stratigraphic distribution of sample groups in the *Aulacostephanus mutabilis* Zone in the Ursental-Risiberg section. Explanations: Fig. 9.

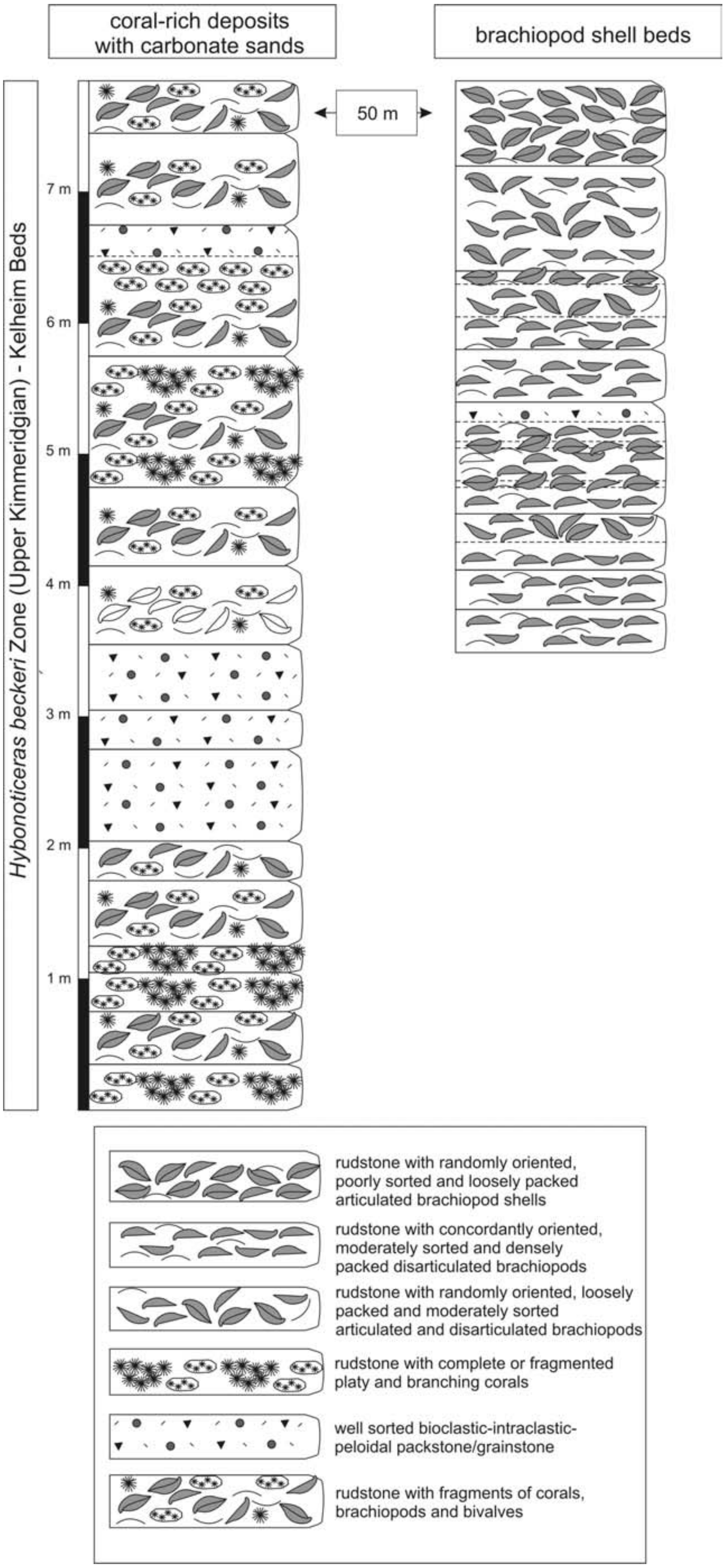


Figure 12 - Brachiopod shell beds dominated by the terebratulid *Juralina insignis* in the Saal section (*Hybonoticeras beckeri* Zone) are laterally replaced by coral thickets, coral debris and carbonate sands.

Discrimination of sample groups

The Q-mode cluster analysis based on untransformed relative abundances and using group-average linking method discriminated 13 sample groups at a Bray-Curtis similarity of approximately 40-50 (Fig. 13). The analysis was based on 94 samples with 7660 individuals. Three samples dominated by the brachiopods *Lacunosella pseudodecorata, Monticlarella strioplicata* and *Monticlarella striocincta* were unique in composition. Twelve groups are dominated by pedunculate brachiopods and one group is dominated by the epibyssate bivalve *Aulacomyella* sp. (Figs. 14-15). Several mudstones and marls that contained less than 25 individuals were dominated by nuculoid bivalves but these samples were not analysed.

(1) The *Lacunosella cracoviensis* sample group is represented by three samples with 261 individuals. The sample-level richness is between 9 and 14, the evenness (PIE) is moderately high (0.59-0.71). The groups is dominated by the pedunculate brachiopod *Lacunosella cracoviensis* (58%), followed by less common *Loboidothyris zieteni* (6.7%) and *Monticlarella striocincta* (4.8%). Cementing pseudolamellibranchs are represented by *Actinostreon gregareum* (3.9%). Shallow burrowing protobranchs are mainly represented by *Isoarca* sp. A and *Isoarca* sp. B. Cementing and epibyssate filibranchs and shallow burrowing eulamellibranchs are rare (< 1%). This group occurs in marly limestones and limestones with sponge and sponge-microbial substrates. It is recorded from the Oxfordian (*E. bimammatum* Zone) and Lower Kimmeridgian (*A. hypselocyclum* Zone).

(2) The *Lacunosella sparsicosta* sample group is defined on the basis of 13 samples with 1814 individuals. Its sample-level richness ranges between 8 and 22, the evenness (PIE) is moderate to high (0.49-0.85). It is dominated by the pedunculate brachiopods *Lacunosella sparsicosta* (44.3%) and *Loboidothyris zieteni* (10%). *Monticlarella triloboides* (6.9%), *Lacunosella multiplicata* (6.7%) and *Nucleata nucleata* (6.3%) are less common. Cementing filibranchs are represented mainly by *Atreta* sp. (5.6%) and epibyssate filibranchs by *Aulacomyella* sp. (1.8%). Shallow burrowing protobranchs (1.6%) and eulamellibranchs (1.5%) are rare and other bivalve guilds do not exceed 1% in terms of their relative abundance. This groups is limited to marly limestones with sponges and limestones with sponge-microbial substrates. It occurs in the Lower Kimmeridgian *S. platynota* and *A. hypselocyclum* zones.

(3) The *Lacunosella multiplicata* sample group consists of seven samples with 365 individuals that are bounded to the Lacunosabänke Member of the Lacunosamergel Formation (*A. hypselocyclum* Zone, Lower Kimmeridgian). The sample-level richness attains 5 to 11 species, the evenness (PIE) is variable (0.33-0.84). The pedunculate brachiopods *Lacunosella multiplicata* (59.6%) and *Loboidothyris zieteni* (10.8%) are most abundant, followed by the small-sized brachiopods *Monticlarella triloboides* (7.3%), *M. striocincta* (5.8%), *Zittelina orbis* (5.7%) and *Nucleata nucleata* (3.6%). Bivalves are rare and mainly represented by epibyssate filibranchs (*Spondylopecten* sp., 2%), shallow burrowing protobranchs (*Isoarca* sp. A, 1%), and cementing filibranchs (*Atreta* sp., 0.5%). This group is invariably limited to sponge-microbial boundstones.

(4) The *Lacunosella polita* sample group being represented by five samples and 578 individuals is derived from the Ursental-Risiberg section that belongs to the *A. mutabilis* Zone (Upper Kimmeridgian). The sample-level richness ranges between 5 and 7 species and the evenness (PIE) is low to moderate (0.2-0.6). In addition to the most abundant brachiopod *Lacunosella polita* (71.9%), the terebratulids *Aulacothyropsis impressula* (10%) and *Loboidothyris zieteni* (8.6%) are common. Other brachiopod species are less common (< 3%). Cementing filibranchs are represented by *Atreta*

sp. (1.5%). Other bivalve guilds are rare (< 1%). This group occurs in marly limestones and limestones with sponge-microbial and sponge-tuberoid substrates.

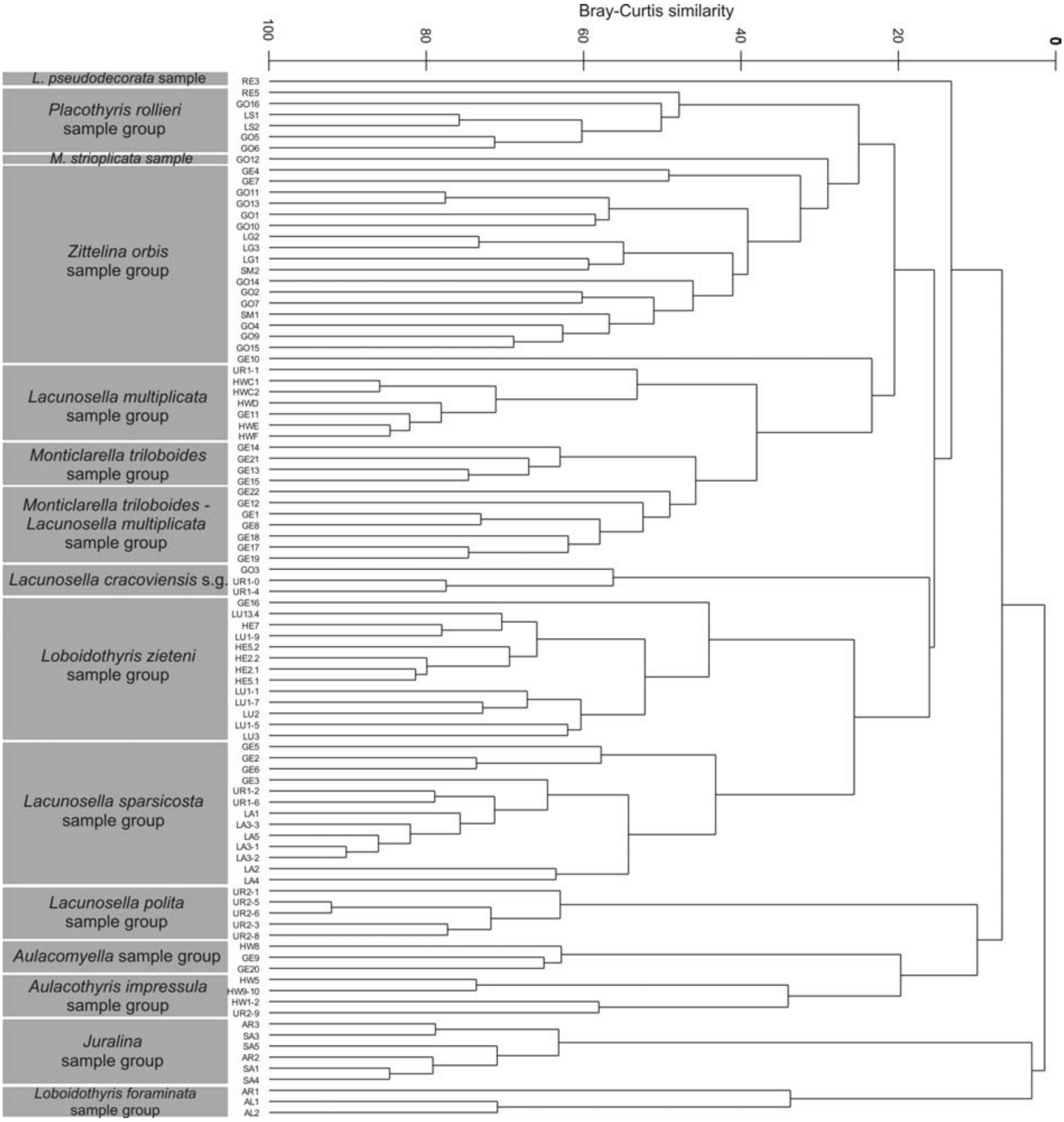


Figure 13 - 13 sample groups and two samples unique in composition discriminated by cluster analysis.

(5) The *Monticlarella triloboides* sample groups consists of four samples and 296 individuals that occur in the *Crussoliceras divisum* Zone (Lower Kimmeridgian, Geisingen section). The sample-level richness is between 6 and 10, the evenness (PIE) is moderate to high (0.59-0.79). The group is dominated by the small-sized rhynchonellid *Monticlarella triloboides* (41.4%) and the small-sized terebratulid *Zittelina orbis* (24.3%). The terebratulids *Loboidothyris zieteni* (11.8%), *Nucleata nucleata* (5.9%) and *Terebratulina striata* (4.9%) are common. Epibyssate filibranchs (4.2%) are mainly represented by *Spondylopecten* sp. (2%) and *Chlamys (Chlamys) textoria* (0.8%), cementing filibranchs by *Atreta* sp. (3.3%), and free-lying filibranchs by *Entolium (Cingentolium)* sp. (1.1%) and

Entolium (Entolium) corneolum (0.6%). Other bivalve guilds are rare (< 1%). The group si limited to marlstones with tuberoids and dispersed sponges.

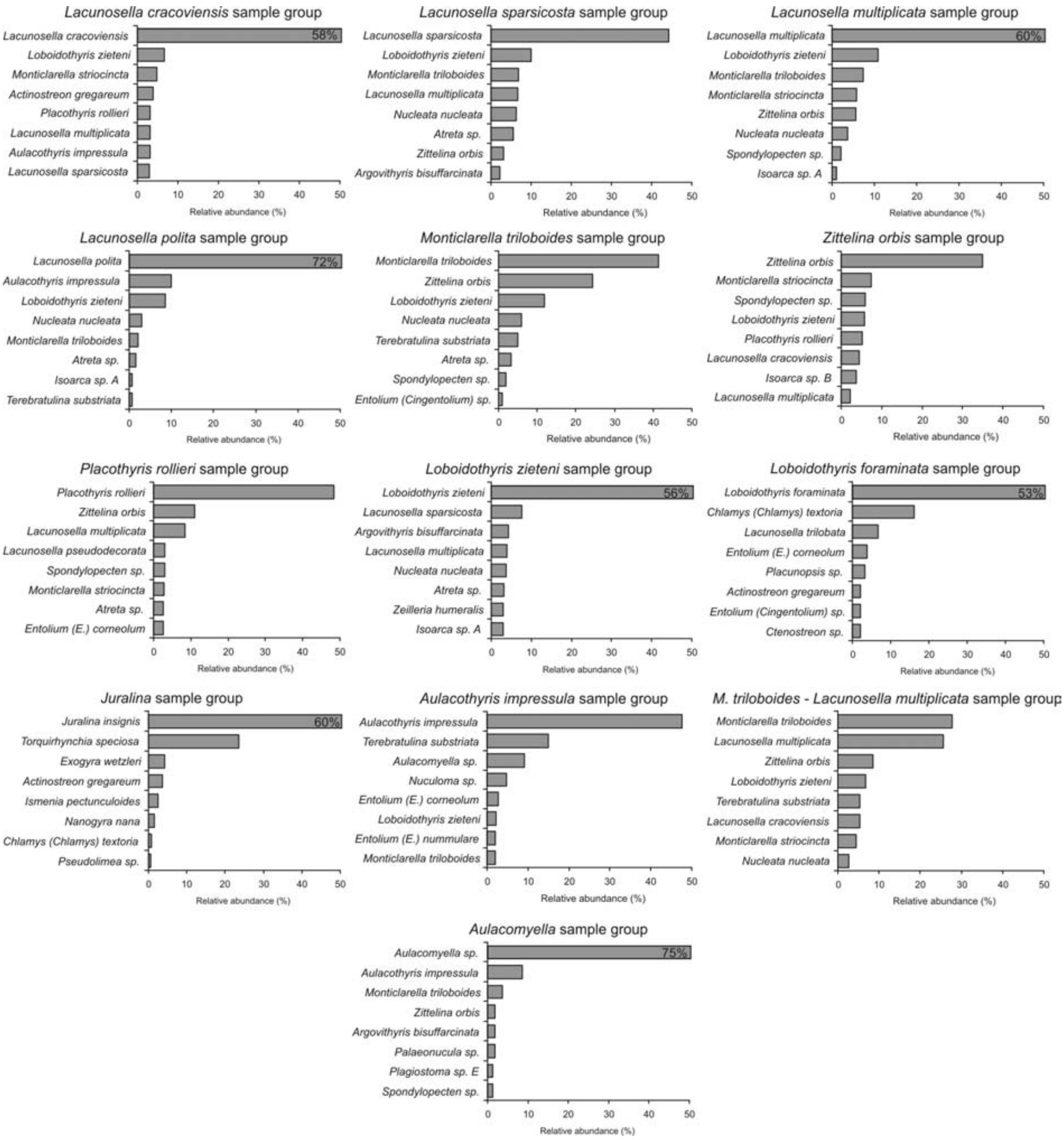
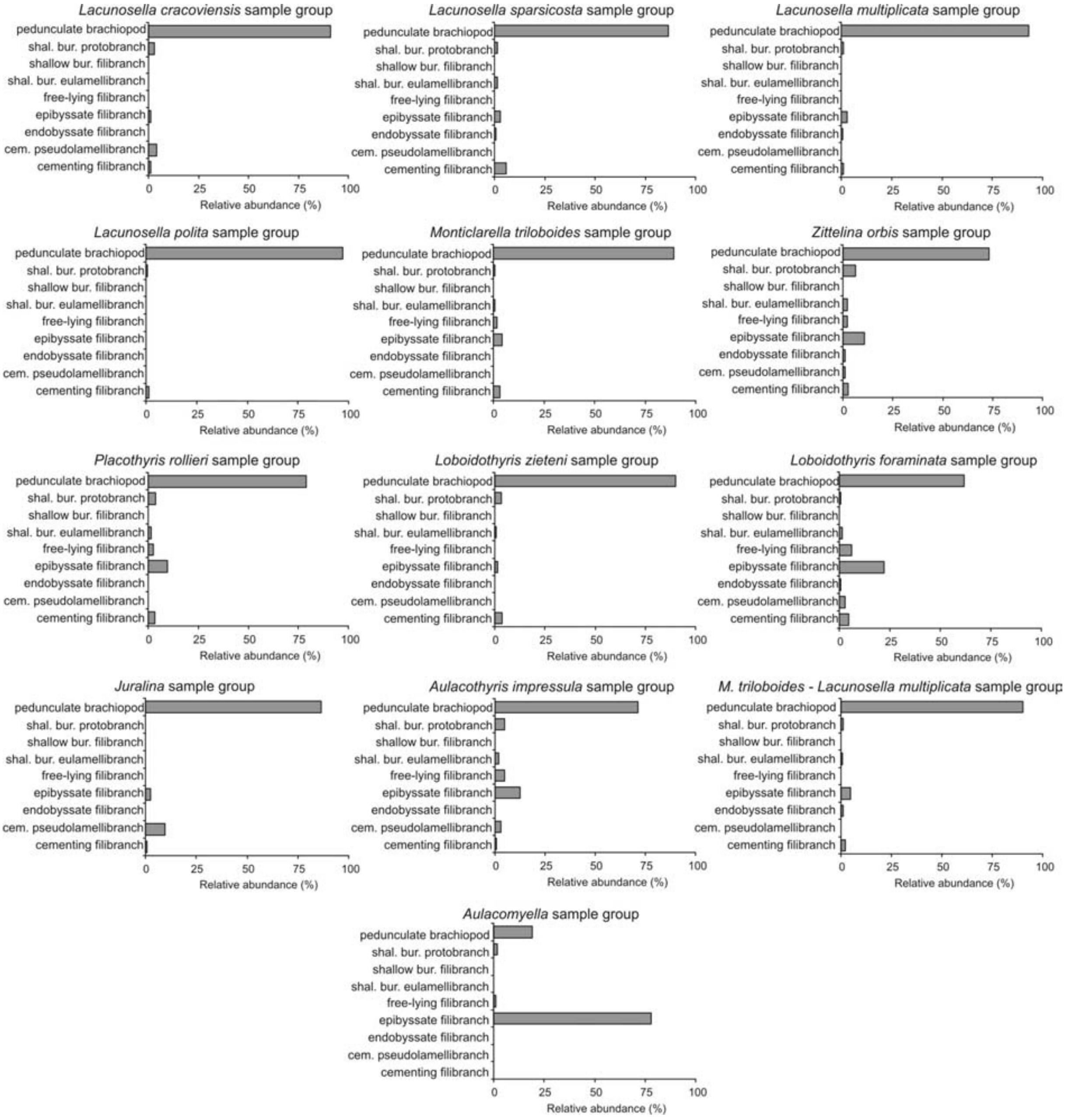


Figure 14 - Relative abundances of the eight most common species in 13 sample groups.

(6) The *Zittelina orbis* sample group is represented by 17 samples with 1050 individuals. Its sample-level richness ranges between 5 and 26 species, the evenness (PIE) is mostly relatively high (0.73-0.91). Two samples are characterized by the lower evenness (0.38-0.48). It is dominated by the small-sized terebratulid *Zittelina orbis* (34.9%), followed by the common brachiopods *Monticlarella striocincta* (7.4%), *Loboidothyris zieteni* (5.7%), *Placothyris rollieri* (5.2%), and *Lacunosella cracoviensis* (4.5%). Bivalves are relatively common, being represented mainly by epibssate filibranchs (11%), shallow burrowing protobranchs (6.4%), cementing filibranchs (2.7%), shallow burrowing eulamellibranchs (2.3%), and free-lying filibranchs (2.1%). This groups is limited to marlstones or marly limestones with substrates represented by dispersed sponges, tuberoids and mud.


Lacunosella cracoviensis sample group

Lacunosella sparsicosta sample group

Lacunosella multiplicata sample group

Lacunosella polita sample group

Monticlarella triloboides sample group

Zittelina orbis sample group

Placothyris rollieri sample group

Loboidothyris zieteni sample group

Loboidothyris foraminata sample group

Juralina sample group

Aulacothyris impressula sample group

M. triloboides - *Lacunosella multiplicata* sample group

Aulacomyella sample group

Figure 15 - Relative abundances of brachiopod and bivalve guilds in 13 sample groups.

(7) The *Placothyris rollieri* sample group is defined on the basis of six samples and 266 individuals that occur in the Oxfordian *E. bimammatum* and Lower Kimmeridgian *S. planula* zones. The sample-level richness is between 6 and 12 species, the evenness (PIE) is moderate to high (0.51-0.84). The terebratulid *Placothyris rollieri* (48.4%) is most abundant. It is followed by relatively common *Zittelina orbis* (11%) and *Lacunosella multiplicata* (8.4%). Epibyssate filibranchs are also common (9.5%), being represented mainly by *Spondylopecten* sp. (2.9%), *Plagiostoma* sp. E (2%), *Chlamys (C.) textoria* (1.7%), and *Aulacomyella* sp. (1.2%). Cementing filibranchs are represented mainly by *Atreta* sp. (2.7%), shallow burrowing protobranchs by *Isoarca* sp. A (1.9%) and *Isoarca* sp. B (1.8%), and free-lying filibranchs by *Entolium (E.) corneolum* (2.5%). This groups occurs in limestones and marly limestones with substrates formed by sponges, sponge-microbial crusts and tuberoids.

(8) The *Loboidothyris zieteni* sample group consists of 13 samples and 878 individuals. Its sample-level richness ranges between 6 and 13 species, the evenness (PIE) is moderate (0.41-0.83). It is dominated by the terebratulid *Loboidothyris zieteni* (56.4%), followed by less common *Lacunosella sparsicosta* (7.6%), *Argovithyris bisuffarcinata* (4.2%), *Lacunosella multiplicata* (3.9%), *Nucleata nucleata* (3.6%), and *Zeilleria humeralis* (3%). Cementing filibranchs are represented by *Atreta* sp. (3.2%) and *Plicatula* sp. (0.6%). Shallow burrowing protobranchs are represented mainly by *Isoarca* sp. A (2.9%). Other bivalve guilds are rare (< 2%). This group occurs mostly in marlstones and marly limestones with sponge and sponge-microbial substrates. It is common mainly in the *S. planula* and *S. platynota* zones, two samples are derived from the *A. hypselocyclum* and *C. divisum* zones.

(9) The *Loboidothyris foraminata* sample group is represented by three samples with 139 individuals. The sample-level richness is between 5 and 13 species, the evenness (PIE) is moderate to high (0.44-0.86). The group is dominated by the terebratulid *Loboidothyris foraminata* (52.6%). The rhynchonellid *Lacunosella trilobata* (6.8%) is less common. The epibyssate filibranchs (22.3%) are relatively abundant, being represented mainly by *Chlamys (C.) textoria* (16.2%). Free-lying filibranchs (5.9%) are represented by *Entolium (E.) corneolum* (3.8%) and *Entolium (Cingentolium)* sp. (2.1%), cementing filibranchs by *Placunopsis* sp. (3.3%) and *Plicatula* sp. (1.4%), and cementing pseudolamellibranchs by *Actinostreon gregareum* (2.1%) and *Nanogyra nana* (0.7%). Other bivalve guilds are rare (< 1.5%). This group is limited to sponge-microbial boundstones of the *Hybonoticeras beckeri* Zone (Upper Kimmeridgian).

(10) The *Juralina* sample group consists of six samples with 787 individuals. The sample-level richness is between 5 and 11 species, the evenness (PIE) is moderate to high (0.42-0.75). One sample from the Saal section has the very low evenness (0.18). The group is dominated by the terebratulid *Juralina insignis* (60.1%) and the rhynchonellid *Torqirhynchia incostans* (23.5%). Other brachiopods are represented by *Ismenia pectunculoides* (2.4%) and *Terebratulina substriata* (0.4%). Bivalves are represented mainly by cementing pseudolamellibranchs (9.5%, *Exogyra wetzleri*, *Actinostreon gregareum, Nanogyra nana*) and epibyssate filibranchs (2.5%, *Chlamys [C.] textoria*, *Pseudolimea* sp., *Eopecten* sp.). Other bivalve guilds are rare (< 1%). This group is limited to bioclastic rudstones of the *Hybonoticeras beckeri* Zone (Upper Kimmeridgian).

(11) The *Aulacothyris impressula* sample group is defined on the basis of four samples and 246 individuals. Its sample-level richness ranges between 6 and 13 species, the evenness (PIE) is variable (0.38-0.82). It is dominated by the small-sized terebratulids *Aulacothyris impressula* (47.7%) and *Terebratulina substriata* (14.9%). Bivalves are relatively common. Epibyssate filibranchs are mainly represented by *Aulacomyella* sp. (9.2%), *Grammatodon (G.)* sp. (1.2%) and *Eopecten* sp. (1%), shallow burrowing protobranchs by *Nuculoma* sp. (4.8%), and free-lying filibranchs by *Entolium (E.) corneolum* (2.7%) and *Entolium (E.) nummulare* (2%). Cementing pseudolamellibranchs are represented by *Liostrea* sp. (1.6%), *Actinostreon gregareum* (0.8%), and *Nanogyra nana* (0.6%). This groups is limited to marly limestones and marlstones with micrite-rich and tuberoid-rich substrates. It occurs in the Oxfordian (*E. bimammatum* Zone), Lower Kimmeridgian (*A. hypselocyclum* Zone) and Upper Kimmerdgian (*A. mutabilis* Zone).

(12) *Monticlarella triloboides-Lacunosella multiplicata* sample group consists of seven samples with 682 individuals. Its sample-level richness attains between 8 and 18 species, the evenness (PIE) is moderate to high (0.64-0.86). The brachiopods *Monticlarella triloboides* (27.8%) and *Lacunosella multiplicata* (25.6%) are the most abundant species, followed by less common brachiopods such as *Zittelina orbis* (8.6%), *Loboidothyris zieteni* (6.8%), *Terebratulina substriata* (5.3%), *Lacunosella cracoviensis* (5.3%), *Monticlarella striocincta* (4.4%), *Nucleata nucleata* (2.6%),

and *Argovithyris bisuffarcinata* (1.9%). Bivalves are mainly represented by epibyssate filibranchs (4.7%), endobyssate filibranchs (1.2%), and shallow burrowing protobranchs (1.2%). This groups typically occurs in marly limestones and limestones with sponges (*A. hypselocyclum* Zone, Lower Kimmeridgian).

(13) The *Aulacomyella* sample group is represented by three samples with 150 individuals. The sample-level richness is between 2 and 9 species, the evenness (PIE) is very low to moderate (0.01-0.58). It is heavily dominated by the epibyssate bivalve Aulacomyella sp. (74.9%), followed by the less common brachiopods *Aulacothyropsis impressula* (8.6%), *Monticlarella triloboides* (3.7%), *Zittelina orbis* (1.9%), and *Argovithyris bisuffarcinata* (1.9%). Shallow burrowing protobranchs (1.9%) and free-lying filibranchs are rare (1%). The group occurs in mud-rich marlstones and is limited to the *Ataxioceras hypselocyclum* Zone of the Lower Kimmeridgian.

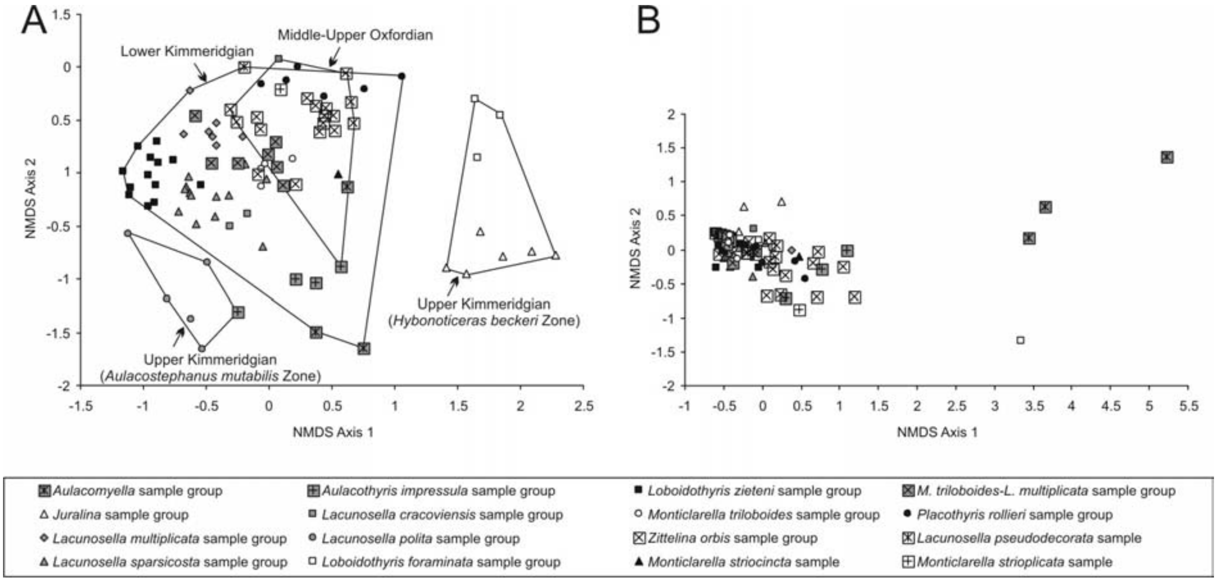


Figure 16 - Compositional relationship among the Oxfordian and Kimmeridgian samples of the southern Germany based on species and guild abundances. A. Q-mode non-metric multidimensional scaling (NMDS) of 94 samples based on species abundances. B. Q-mode NMDS of 94 samples based on guild abundances. Note that stratigraphic segregation follows from species but not guild composition.

Ordination of the Oxfordian-Kimmeridgian samples and temporal turnover

Ordination of samples in Q-mode non-metric multidimensional scaling (NMDS) based on species abundances is showing gradual compositional transitions and high overlap between the Oxfordian and Lower Kimmeridgian samples (Fig. 16A). Sample groups from the Upper Kimmeridgian *Aulacostephanus mutabilis* (*Lacunosella polita* sample group) and *Hybonoticeras beckeri* zones (*Loboidothyris foraminata* and *Juralina* sample groups) are compositionally segregated from the Oxfordian and Lower Kimmeridgian samples. Among the Oxfordian and Lower Kimmeridgian sample groups, the bivalve-dominated *Aulacomyella* sample group and the *Aulacothyropsis* sample groups are partly segregated from other brachiopod-dominated sample groups. Q-mode NMDS based on guild abundances shows a marked feature of the guild structure of Late Jurassic benthic communities of the Southern Germany – 90 samples are strongly clustered because they are heavily dominated by pedunculate brachiopods (Fig. 16B). Three samples dominated by the epibyssate bivalve *Aulacomyella* sp. and one sample of the *Loboidothyris foraminata* sample group with abundant epibyssate bivalves are strongly segregated from brachiopod-dominated samples.

One-way analysis of similarities (ANOSIM) testing differences among stratigraphic zones shows that there was a significant temporal turnover in species composition (R = 0.54, p < 0.0001). With the exception of insignificant differences between the *D. bifurcatus* and *E. bimammatum* zones, and between the *A. hypselocyclum* and *C. divisum* zones, all pairwise comparisons are characterized by significance levels < 0.05. In contrast, differences among stratigraphic zones based on guild abundances minimal and insignificant (R = 0.068, p = 0.11).

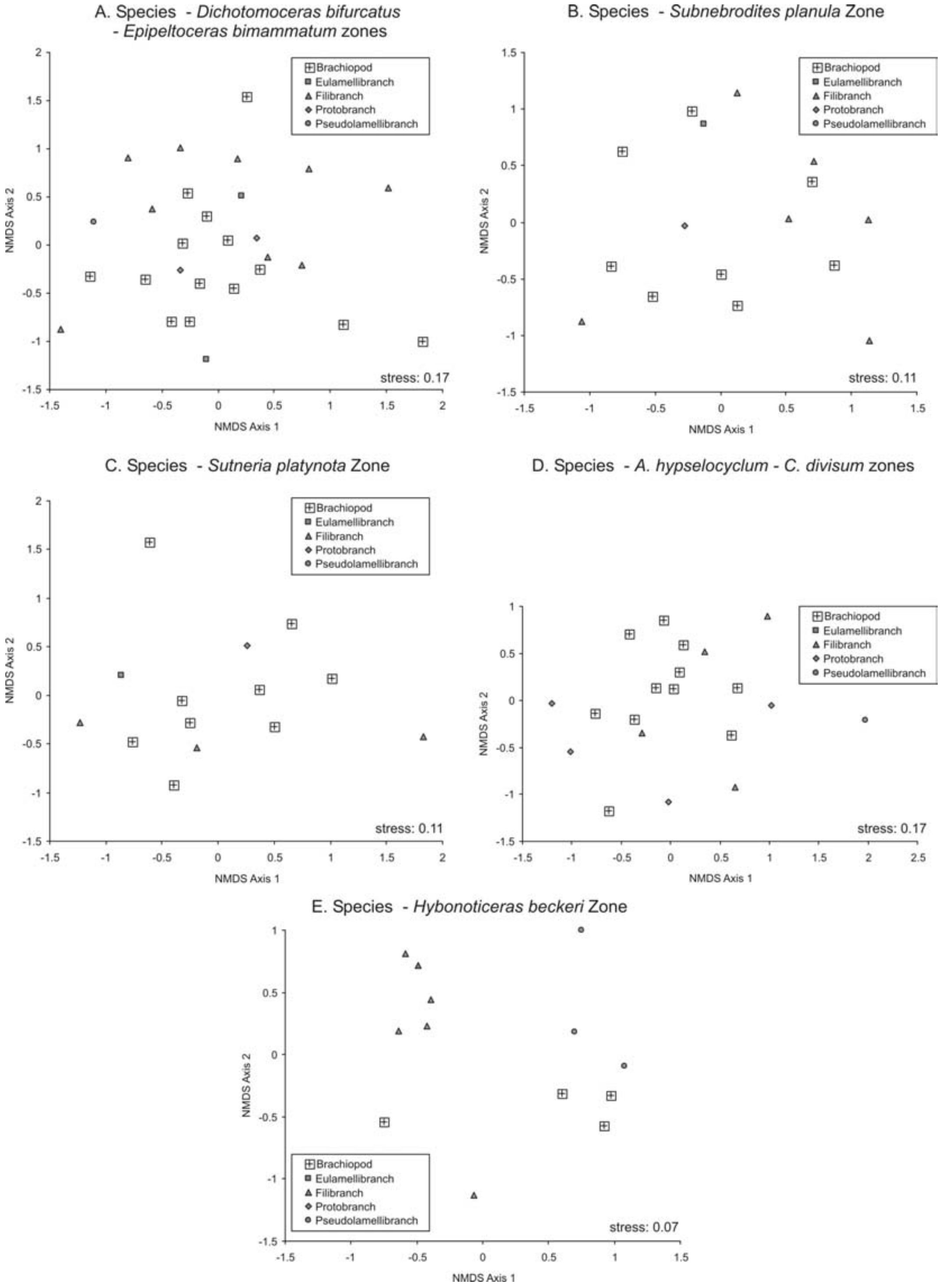


Figure 17 - Abundance patterns of brachiopod and bivalve species in R-mode non-metric multidimensional scaling (NMDS). A. The *Dichotomoceras bifurcatus – Epipeltoceras bimammatum* zones. B. The *Subnebrodites planula* Zone. C. The *Sutneria platynota* Zone. D. The *Ataxioceras hypselocyclum – Crussoliceras divisum* zones. E. The *Hybonoticeras beckeri* Zone.

R-mode based one-way ANOSIM testing differences in species abundance among guilds	R	p-value	Number of permutations	Number of permuted R≥observed R
Dichotomoceras bifurcatum - Epipeltoceras bimammatum zones	0.025	0.373	10000	3731
Subnebrodites planula Zone	-0.043	0.632	10000	6318
Sutneria platynota Zone	0.072	0.34	10000	3401
Ataxioceras hypselocyclum - Crussoliceras divisum zones	0.326	0.0039	10000	39
Hybonoticeras beckeri Zone	0.325	0.016	10000	159

Table 1 - Analyses of similarities (ANOSIM) testing differences in abundance patterns among protobranchs, filibranchs, pseudolamellibranchs, eulamellibranchs and brachiopods. This test is performed separately for five time intervals.

Co-occurrence patterns of brachiopods and bivalves

R-mode NMDS (Fig. 17) and analysis of similarities (ANOSIM) based on abundances of species > 5% per sample gives different results for five investigated time intervals. Species abundance patterns among brachiopods and four simplified bivalve guilds (i.e., protobranchs, filibranchs, pseudolamellibranchs, and eulamellibranchs) are minimal and insignificant for assemblages from the Oxfordian, the *S. planula* Zone and the *S. platynota* Zone (Tab. 1). In contrast, species abundance patterns among brachiopod and bivalve guilds significantly differed in the *A. hypselocyclum – C. divisum* zones ($R = 0.33$, $p = 0.004$) and the *H. beckeri* Zone ($R = 0.33$, $p = 0.016$). Partial segregation of brachiopods and bivalve guilds in these two time intervals is also visible in R-mode NMDS (Fig. 17D-E). Pairwise comparisons show that in the *A. hypselocyclum – C. divisum* zones, the main difference is lying between abundances of brachiopods and protobranch bivalves ($R = 0.37$, $p = 0.007$). In the *H. beckeri* Zone, the differences between brachiopods and filibranchs ($R = 0.3$, $p = 0.043$), and between pseudolamellibranchs and filibranchs ($R = 0.6$, $p = 0.036$) are of borderline significance.

Effects of siliciclastic supply

Dichotomoceras bifurcatus – Epipeltoceras bimammatum zones. As follows from ANOSIM (Tab. 2) and Q-mode NMDS (Fig. 18), communities significantly differ in species composition among habitats differing in the siliciclastic supply ($R = 0.27$, 0.015). In contrast, there are no significant differences in guild composition among marls, marly limestones and limestones (Tab. 2, $R = -0.024$, $p = 0.53$). The small-sized dallinid brachiopod *Zittelina orbis* decreased and the large-sized brachiopods *Lacunosella, Placothyris* and *Loboidothyris* increased in abundance with increasing carbonate supply. Pedunculate brachiopods thus dominated across the whole gradient with varying sediment supply, although bivalves slightly increased in abundance and guild richness towards marls (Fig. 19).

Subnebrodites planula Zone. Habitats differing in the siliciclastic supply highly and significantly vary in species community composition ($R = 0.98$, $p = 0.008$, Tab. 3). The differences in guild community composition are minimal and insignificant ($R = 0.19$, $p = 0.063$, Tab. 3). Species differences are mainly related to between-species variations in abundance of terebratulids. *Loboidothyris zieteni* dominated in marly limestones and *Placothyris rollieri* dominated in limestones (Fig. 20) . Bivalve guilds were rare. Epibyssate and free-lying bivalves slightly increased in abundance towards limestones.

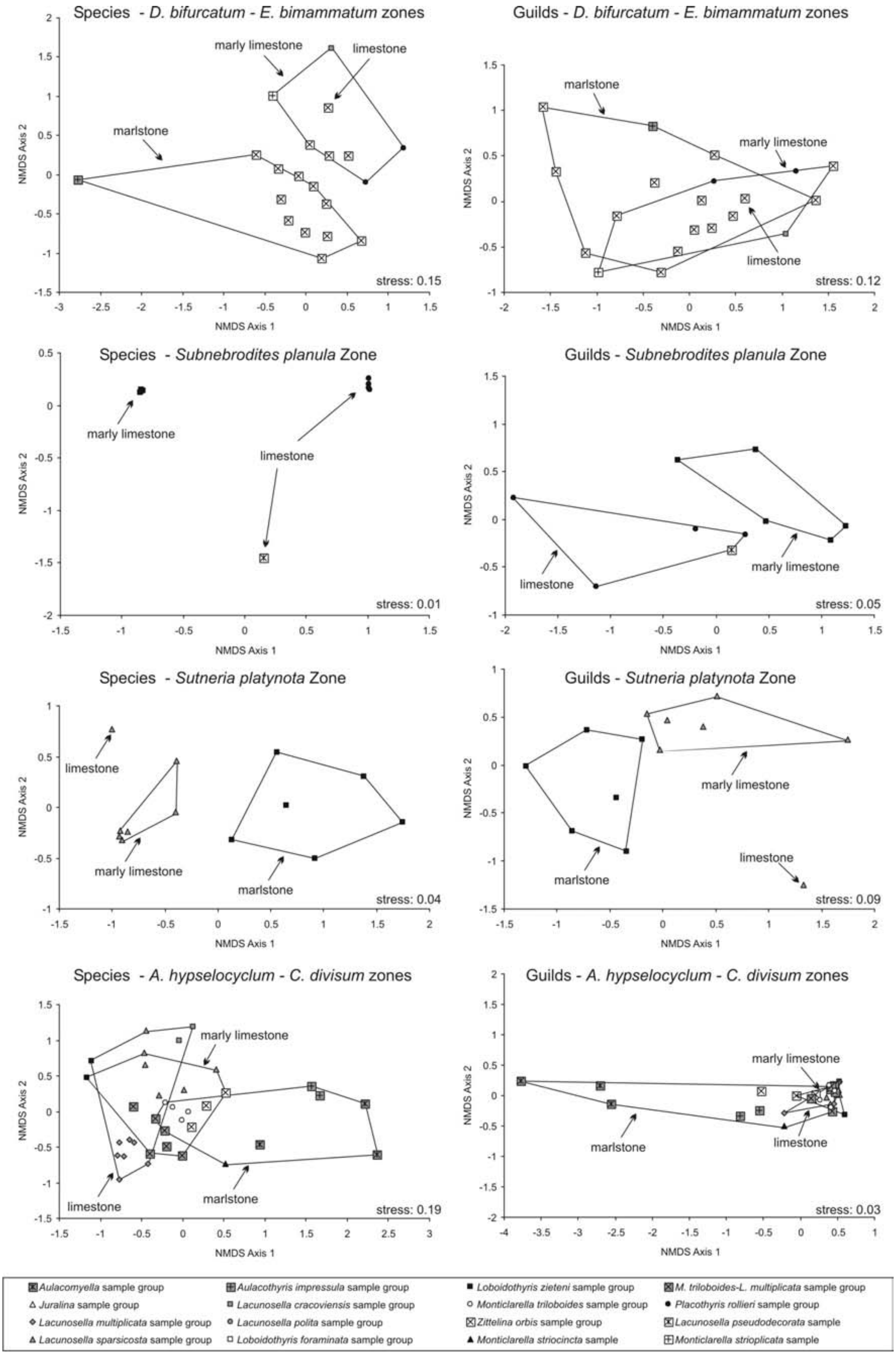


Figure 18 - Q-mode non-metric multidimensional scaling (NMDS) based on species and guild abundances visualizing differences in community composition between habitats differing in the siliciclastic supply during (1) the *Dichotomoceras bifurcatus – Epipeltoceras bimammatum* zones, (2) the *Subnebrodites planula* Zone, (3) the *Sutneria platynota* Zone, and (4) and the *Ataxioceras hypselocyclum – Crussoliceras divisum* zones.

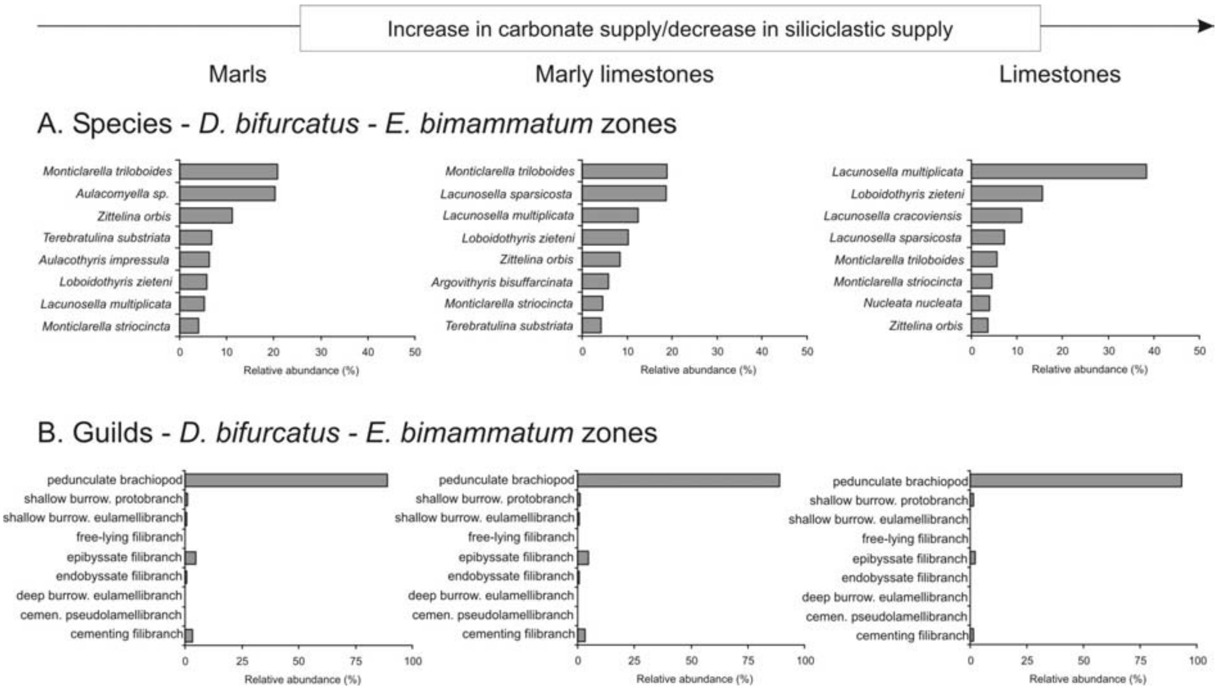


Figure 19 - Between-habitat differences in abundances of species and guilds with respect to varying siliciclastic/carbonate supply in the *Dichotomoceras bifurcatus – Epipeltoceras bimammatum* zones.

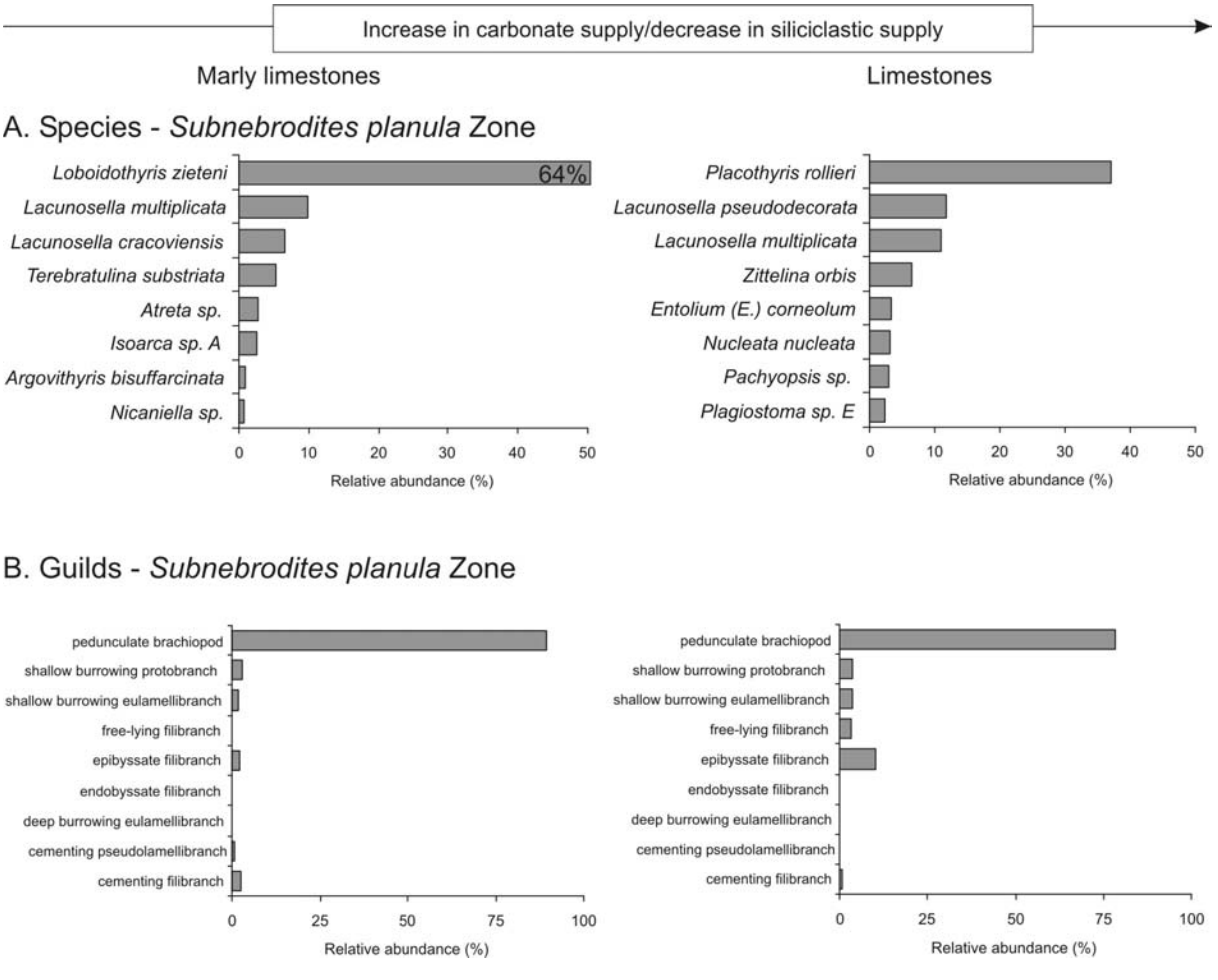


Figure 20 - Between-habitat differences in abundances of species and guilds with respect to varying siliciclastic/carbonate supply in the *Subnebrodites planula* Zone.

Sutneria platynota Zone. Both species (R = 0.88, p = 0.0002, Tab.4) and guild composition (R = 0.54, p = 0.0005) are significantly different between marls and marly limestones. Similarly as in the *S. planula* Zone, *Loboidothyris zieteni* increased in abundance towards marl-rich habitats (Fig. 21). *Lacunosella sparsicosta* dominated in limestones. Abundance of cementing filibranchs slightly increased towards limestones.

Ataxioceras hypselocyclum – Crussoliceras divisum zones. There are very low but significant differences in species composition among marls, marly limestones and limestones (R = 0.19, p = 0.005, Tab. 5). The differences in guild composition are minimal and insignificant (R = 0.06, p = 0.08, Tab. 5). Q-mode NMDS visualizing between-habitat differences shows high variation in guild composition of marls (Fig. 18). Some marls are dominated by the bivalve *Aulacomyella* sp., but other marl-rich samples are dominated by pedunculate brachiopods and thus group together with marly limestones and limestones. Similarly as in the Oxfordian, abundance of the small-sized brachiopods such as *Zittelina orbis* and *Monticlarella triloboides* decreased with increasing carbonate supply (Fig. 22). In contrast, abundance of te large-sized brachiopods *Lacunosella* and *Loboidothyris* increased with increasing carbonate supply. In general, abundance of pedunculate brachiopods slightly decreased and of epibyssate bivalves (*Aulacomyella*) increased with increasing siliciclastic supply.

Hybonoticeras beckeri Zone. Effects of varying siliciclastic/carbonate supply were not investigated for this zone because all samples are represented by pure limestones.

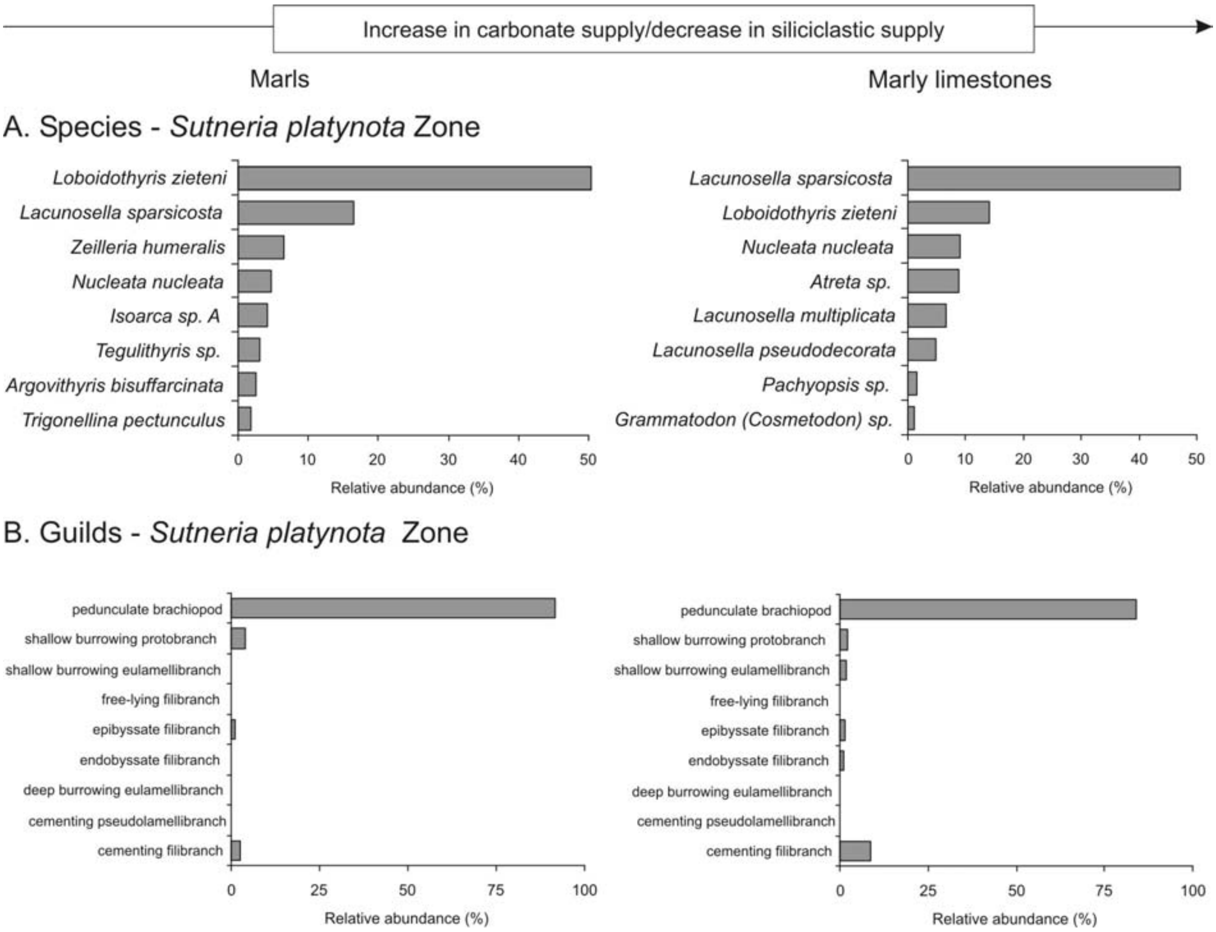


Figure 21 - Between-habitat differences in abundances of species and guilds with respect to varying siliciclastic supply in the *Sutneria platynota* Zone.

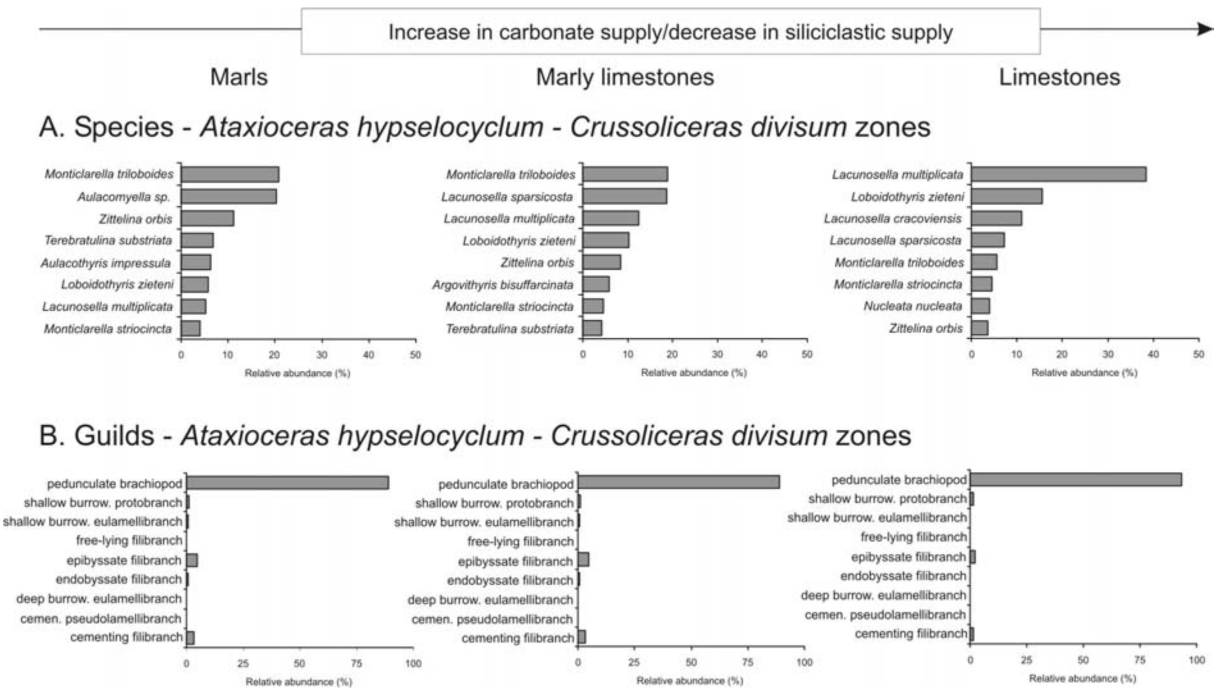


Figure 22 - Between-habitat differences in abundances of species and guilds with respect to varying siliciclastic supply in the *Ataxioceras hypselocyclum – Crussoliceras divisum* zones.

Effects of substrate consistency

Dichotomoceras bifurcatus – Epipeltoceras bimammatum zones. There are relatively low but significant differences in species composition among habitats differing in the substrate consistency (ANOSIM, R = 0.23, 0.001, Tab. 2). The differences in guild composition and minimal and insignificant (R = 0.04, p = 0.23). Mixed substrate formed by marls with tuberoids were dominated by the small-sized brachiopods *Zittelina orbis* and *Monticlarella striocincta* (Fig. 23). Hard substrates formed by sponges with microbial crusts were mainly inhabited by *Zittelina orbis*, but also by the large-sized brachiopods *Placothyris rollieri* and *Lacunosella cracoviensis*. Abundances of brachiopods and epifaunal and infaunal bivalves do not show any substantial differences between mixed and hard substrates.

Subnebrodites planula Zone. In this time interval, habitats differing in the substrate consistency show relatively high and significant differences both in species (R = 0.61, p = 0.008, Tab. 3) and guild composition (R = 0.5, p = 0.05). *Loboidothyris zieteni* dominated on hard substrates with sponges and *Placothyris rollieri* was abundant mainly on substrates with mixture of sponge and crust fragments (Fig. 24). Abundance of pedunculate brachiopods decreased and of shallow burrowing, epibyssate, and free-lying bivalves increased with decreasing substrate consistency. When sponge substrates are compared with sponge-microbial crust substrates, there are also high differences in species composition, with *L. zieteni* being dominant on the first substrate type and *P. rollieri* on the second substrate type.

Sutneria platynota Zone. Effects of varying substrate consistency on community composition were not investigated for this zone because all samples are represented by sponge-rich hard substrates.

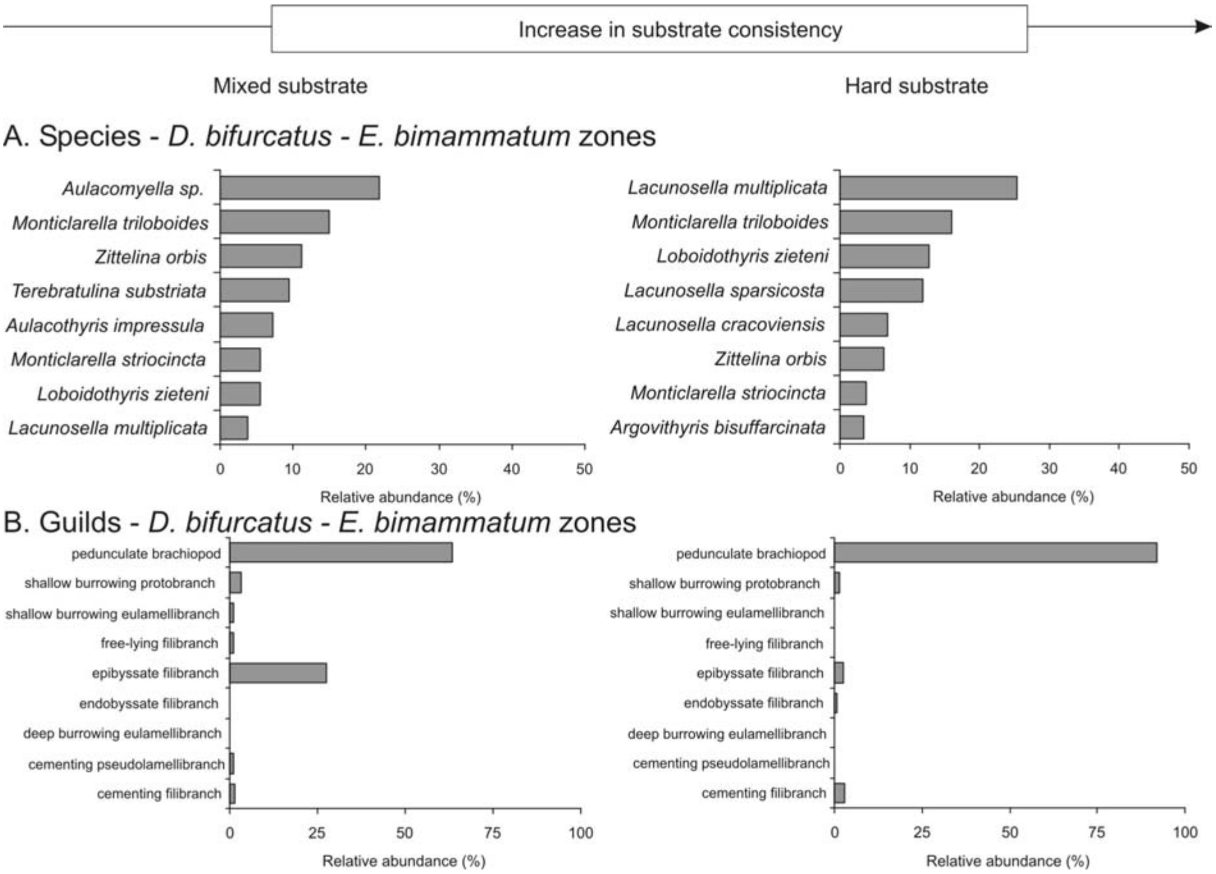


Figure 23 - Between-habitat differences in abundances of species and guilds with respect to varying substrate consistency in the *Dichotomoceras bifurcatus – Epipeltoceras bimammatum* zones.

Ataxioceras hypselocyclum – Crussoliceras divisum zones. The differences in sample-level species composition between hard and mixed substrates are relatively low and significant (R = 0.29, p = 0.0014, Tab. 5). The differences in sample-level guild composition between hard and mixed substrates are higher that those based on species composition (R = 0.49, p < 0.0001). The epibyssate bivalve *Aulacomyella* sp. and the small-sized brachiopods *Zittelina orbis*, *Terebratulina substriata*, *Aulacothyris impressula* and *Monticlarella striocincta* were most abundant on mixed substrates (Fig. 25). In contrast, the large-sized brachiopods *Lacunosella* and *Loboidothyris* dominated on hard substrates. *Monticlarella triloboides* was relatively abundant on both substrate types. The between-substrate differences in guild composition are mainly related to lower abundane of brachiopods and higher abundance of epibyssate bivalves on mixed than on hard substrates. There are also some differences in species composition between sponge and sponge-microbial crust substrates (R = 0.24, p = 0.0039). Sponges were mainly inhabited by the rhynchonellid *Montoliclarella triloboides* and sponge-microbial crusts by the rhynchonellid *Lacunosella*.

Hybonoticeras beckeri Zone. The differences between hard substrates formed by sponges and crusts and mixed-bottom substrates formed by skeletal sand are high both for species (R = 1, p = 0.012, Tab. 6) and guild composition (R = 0.5, p = 0.036). Pedunculate brachiopods decreased and epibyssate bivalves increased in abundance with increasing substrate consistency. *Loboidothyris foraminata* inhabited sponge-microbial crust substrates, and *Juralina insignis* and *Torquirhynchia speciosa* dominated on substrates formed by well sorted skeletal sands.

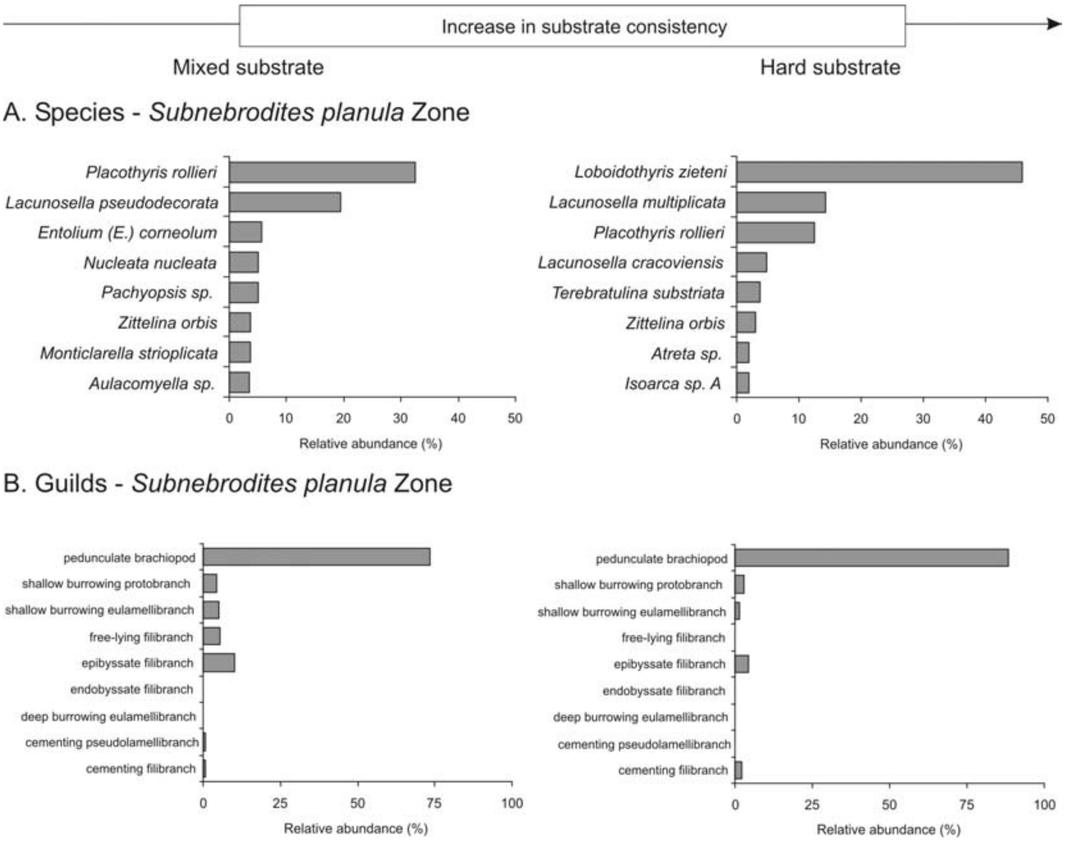


Figure 24 - Between-habitat differences in abundances of species and guilds with respect to varying substrate consistency in the *Subnebrodites planula* Zone.

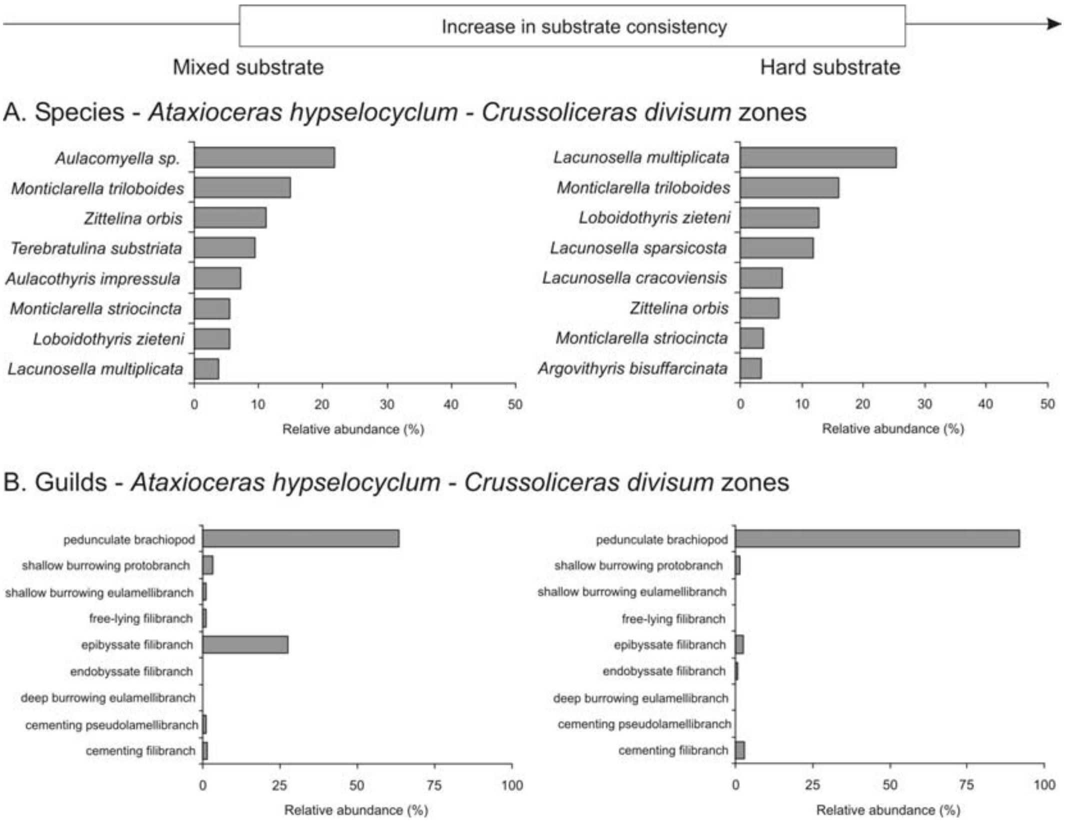


Figure 25 - Between-habitat differences in abundances of species and guilds with respect to varying substrate consistency in the *Ataxioceras hypselocyclum – Crussoliceras divisum* zones.

Effects of wave-base level

This effect was investigated for assemblages of the *Hybonoticeras beckeri* Zone only because assemblages of other zones are derived from relatively uniform environments with respect to wave-base level (i.e., around and below maximum storm wave base). In the *H. beckeri* Zone, two samples are derived from habitats above normal storm wave base and one sample from habitats below normal storm wave base, in contrast to six samples from habitats above fair-weather wave base (FWWB). However, it seems that the between-habitat differences in species composition are consistently high (R = 0.94, p = 0.008, Tab. 6). The brachiopods *Juralina insignis* and *Torquirhynchia speciosa* dominated in the shallowest, high-energy habitats above FWWB (Fig. 26). *Loboidothyris foraminita* and *Chlamys (Chlamys) textoria* were abundant in habitats below FWWB. The differences in guild composition are rather insignificant because all habitats are dominated by pedunculate brachiopods (R = 0.49, p = 0.063).

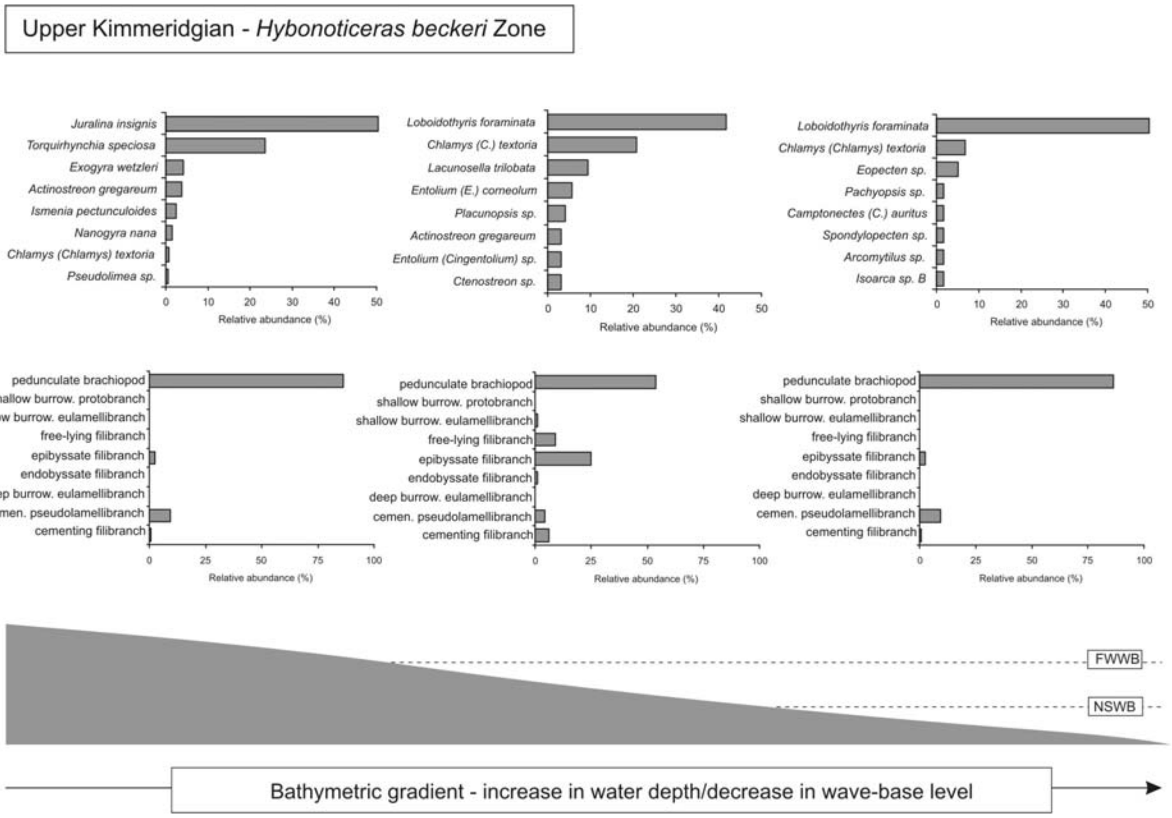


Figure 26 - Between-habitat differences in abundances of species and guilds with respect to varying wave-base level in the *Hybonoticeras beckeri* Zone.

One-way ANOSIM - effect of sediment supply	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.267	0.015	10000	154
marl vs. marly limestone	0.277	0.011	10000	110
Guilds - global test	-0.024	0.53	10000	5310
marl vs. marly limestone	0.046	0.27	10000	2695

One-way ANOSIM - effect of substrate consistency	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - hard vs. mixed substrate	0.232	0.001	10000	10
Guilds - hard vs. mixed substrate	0.038	0.225	10000	2248

Table 2 - One-way analyses of similarities (ANOSIM) testing effects of varying siliciclastic supply and substrate consistency on species and guild composition in the *Dichotomoceras bifurcatus – Epipeltoceras bimammatum* zones.

One-way ANOSIM - effect of sediment supply	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test				
limestone vs. marly limestone	0.98	0.008	126	1
Guilds - global test				
limestone vs. marly limestone	0.188	0.063	126	8

One-way ANOSIM - effect of substrate consistency	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - hard vs. mixed substrate	0.613	0.008	120	1
Guilds - hard vs. mixed substrate	0.5	0.05	120	6

Table 3 - One-way analyses of similarities (ANOSIM) testing effects of varying siliciclastic supply and substrate consistency on species and guild composition in the *Subnebrodites planula* Zone.

One-way ANOSIM - effect of sediment supply	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.888	0.0002	6006	1
marl vs. marly limestone	0.904	0.002	462	1
Guilds - global test	0.536	0.0005	6006	3
marl vs. marly limestone	0.4	0.0043	462	2

Table 4 - One-way analyses of similarities (ANOSIM) testing effects of varying siliciclastic supply on species and guild composition in the *Sutneria platynota* Zone.

One-way ANOSIM - effect of sediment supply	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.19	0.005	10000	5
limestone vs. marly limestone	0.182	0.02	10000	200
limestone vs. marl	0.291	0.0012	10000	12
marly limestone vs. marl	0.092	0.068	10000	682
Guilds - global test	0.055	0.076	10000	756
limestone vs. marly limestone	0.081	0.068	10000	680
limestone vs. marl	0.111	0.044	10000	436
marly limestone vs. marl	0.012	0.287	10000	2869

One-way ANOSIM - effect of substrate consistency	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - hard vs. mixed substrate	0.294	0.0014	10000	14
Guilds - hard vs. mixed substrate	0.492	<0.0001	10000	0

Table 5 - One-way analyses of similarities (ANOSIM) testing effects of varying siliciclastic supply and substrate consistency on species and guild composition in the *Ataxioceras hypselocyclum – Crussoliceras divisum* zones.

One-way ANOSIM - effect of substrate	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - hard-bottom vs. mixed-bottom	1	0.012	84	1
Guilds - hard-bottom vs. mixed-bottom	0.5	0.036	84	3

One-way ANOSIM - effect of wave-base level	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - global test	0.944	0.0080	252	2
Guilds - global test	0.494	0.063	252	16

Table 6 - One-way analyses of similarities (ANOSIM) testing effects of varying wave-base level and substrate consistency on species and guild composition in the *Hybonoticeras beckeri* Zone.

Discussion

Species composition. As follows from environmental analyses, variations in species community composition correlate with variations in siliciclastic supply and substrate consistency. Variations in guild composition are related less strongly to environmental variations with respect to siliciclastic supply and substrate consistency, mainly because pedunculate brachiopods mostly dominate along the whole gradient with varying siliciclastic supply and substrate consistency. The exceptions are soft- to mixed bottom habitats dominated by *Aulacomyella* sp. and some samples with shallow burrowing deposit-feeding bivalves. Differentiation of brachiopod species to habitats differing in substrate consistency followed mainly their size differentiation, with large-sized brachiopods restricted to rich biostromes and mounds and small-sized brachiopods being dominant on mixed substrates with high proportions of mud. This variation implies relatively high ecologic tolerance of brachiopods with respect to varying substrate consistency, although individual species might have ben characterized by narrow tolerances. A small size of benthic invertebrates is assumed to represent one of the strategies for coping with unstable substrates because small-sized individuals with thin shells have lower density and lower total mass, thus preventing their sinking into soft substate (Thayer, 1975).

Guild composition. The Oxfordian and Kimmeridgian brachiopod-bivalve communities of southern Germany are characterized by high dominance of brachiopods. Among bivalves, epifaunal guilds can be locally common but infaunal suspension-feeding guilds are rare or absent. Rarity of infaunal suspension-feeding bivalves as opposed to epifaunal bivalves also follows from quantitative data of Wagenplast (1972), Nitzopoulos (1974) and Werner et al. (1994). Although infaunal suspension-feeding bivalves were obviously limited by high substrate consistency in sponge-microbial communities, their abundance was also minimal on soft substrates. Variations in guild composition are related less strongly to environmental variations with respect to siliciclastic supply and substrate consistency, mainly because pedunculate brachiopods dominate along the whole gradient with varying siliciclastic supply and substrate consistency. However, the epibyssate bivalve *Aulacomyella* sp. and shallow burrowing deposit-feeding bivalves increased towards soft- to mixed-bottom habitats. The epibyssate bivalve *Aulacomyella* sp. belongs to the so-called paper pectens that are commonly inhabitants of soft and/or oxygen-deficient bottoms (Wignall, 1993). The ability of *Aulacomyella* to live in dysaerobic environments was explicitly assumed by Doyle and Whitham (1991) and Kelly and Doyle (1991) because (1) it occurs in organic-rich sediments devoid of other benthos that are supposed to represent oxygen-deficient habitats, (2) it forms paucispecific assemblages (i.e., implying high-stress conditions, possibly owing to low oxygen levels), and (3) it occurs in shell-rich pavements that alternate with shell-poor or barren clays or mudstones (i.e., implying single colonisation events and opportunistic population dynamics as a response to fluctuations in oxygen levels). Short-distance horizontal replacement between sponge-microbial mounds with large-sized brachiopods and marls and mudstones rich in small brachiopods, *Aulacomyella* and *Chondrites* as observed in the Lacunosabänke interval of the *Ataxioceras hypselocyclum* Zone (Fig. 10) imply low oxygen levels and low flow velocity owing to reduced within-basin circulation. This horizontal replacement is constraining effects of varying siliciclastic and carbonate supply because they had to be constant on such small spatial scales and indicates that variations in substrate consistency probably governed the change between communities dominated by large-sized and small-sized brachiopods. Reduced flow velocity and reduced oxygen concentrations thus may account for the specific guild structure of sponge mounds and biostromes with dominance of brachiopods. Infaunal suspension-feeding bivalves with high pumping rates and high metabolic requirements were probably limited even on soft-bottom habitats owing to low flow velocities and low oxygen levels. Low abundance of epifaunal bivalves in hard-bottom habitats of sponge-microbial mounds can be similarly related to such environmental conditions, although epifaunal bivalves have mostly higher clearance rates than infaunal bivalves. They can be thus better adapted to dysaerobic conditions than infaunal suspension-feeding bivalves. Brachiopod dominance in hard-bottom habitats might also be enhanced by reduced oxygen levels because they may limit grazers and competitors for space other than bivalves. Reduced oxygen levels are also commonly invoked to explain high abundance of microbial crusts in sponge-microbial mounds of souther Germany (Leinfelder, 2001).

Conclusions

Variations in siliciclastic supply and substrate consistency had invariably significant effects on abundances of brachiopod and bivalve species that inhabited deep-shelf, sponge habitats in southern Germany during the Late Jurassic. Abundances of guilds correlate with variations in siliciclastic supply in the *Sutneria platynota* Zone only, and with variations in substrate consistency in the *Subnebrodites planula*, *Ataxioceras hypselocyclum-Crussoliceras divisum*, and *Hybonoticeras beckeri* zones. During the Oxfordian and Early Kimmeridgian, large-sized terebratulids and rhynchonellids inhabited hard-bottom habitats represented by sponge biostromes and sponge-microbial mounds. In contrast, small-sized terebratulid and rhynchonellid brachiopods and the epibyssate bivalve *Aulacomyella* were abundant on soft bottoms. Shallow burrowing deposit-feeding bivalves locally occur in shell-poor deposits representing soft-bottom conditions, but their numerical abundance is invariably very low. Infaunal suspension-feeding bivalves were rare on soft bottoms. During the Late Kimmeridgian, environments were more differentiated owing to general shallowing that took place during the Late Jurassic. However, both shallow and deep environments above and below fair-weather wave base were dominated by pedunculate brachiopods.

In the *Ataxioceras hypselocyclum* Zone of the Lower Kimmeridgian, horizontal community replacements between sponge-rich habitats with large-sized brachiopods and mud-rich habitats with small-sized brachiopods, *Aulacomyella* and *Chondrites* on the scale of several decimeters imply that (1) variations in substrate consistency partly governed species and guild abundances, and (2) hard-bottom and soft-bottom communities dominated by brachiopods might be living under oxygen-deficient conditions. Rarity of shallow burrowing suspension-feeding bivalves in sponge habitats might by related to high substrate consistency, but their similarly low abundance in soft-bottom habitats indicates that factors related to low oxygen concentrations and reduced flow velocity in deep-shelf habitats may limit their distribution. Higher abundance of brachiopods than of bivalves in deep-shelf habitats with restricted flow velocities is in accord with the hypothesis proposed for the Sinemurian sponge communities that brachiopods were probably characterized by more efficient feeding strategy to cope with limited flow velocities than bivalves with higher pumping rates. Reduced oxygen levels may also limit grazers and competitors for space other than bivalves, thus enhancing brachiopod dominance.

	LG1	LG2	LG3	SM1	SM2	GO1	GO2	GO3	GO4	GO5	GO6	GO7	GO9	GO10	GO11	GO12	GO13	GO14	GO15
Torquirhynchia speciosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella trilobata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella multiplicata	1	0	3	0	0	2	0	5	0	0	0	0	0	3	2	2	4	0	0
Lacunosella cracoviensis	0	0	0	0	0	12	0	37	2	0	0	12	0	8	4	8	5	3	0
Lacunosella pseudodecorata	0	0	0	0	0	0	0	5	0	0	0	4	0	4	0	0	0	0	0
Lacunosella sparsicosta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella polita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella striocincta	2	0	0	5	3	0	1	3	6	3	1	15	6	2	1	5	0	10	16
Monticlarella czenstochaviensis	0	0	0	0	0	3	0	0	0	0	0	1	3	1	0	0	0	6	5
Monticlarella strioplicata	0	0	0	0	0	3	9	0	1	0	0	9	0	1	0	10	0	5	0
Monticlarella triloboides	0	0	0	0	0	2	1	0	0	1	0	5	0	1	0	0	0	1	1
Juralina insignis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argovithyris bisuffarcinata	0	1	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Placothyris rollieri	5	0	0	0	0	0	27	7	6	22	35	8	1	4	3	1	3	5	0
Loboidothyris zieteni	0	0	0	0	0	11	4	0	0	0	3	0	0	9	5	0	8	0	2
Loboidothyris foraminata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucleata nucleata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonellina loricata	0	0	0	7	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Trigonellina pectunculus	0	1	0	0	4	0	1	0	1	0	0	1	0	0	0	0	0	0	1
Dictyothyris kurri	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Terebratulina substriata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ismenia pectunculoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina orbis	22	43	37	14	36	20	34	2	13	10	7	36	14	5	12	4	17	8	24
Zittelina gutta	0	0	0	0	0	0	8	0	0	1	0	14	1	1	1	0	0	0	0
Zittelina trisignata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria humeralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulacothyris impressula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulacothyris impressa	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tegulithyris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ornithella lampas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	0	0	0	0	5	0	0	0	0	7	1	0	0	0	0	1	0
Palaeonucula sp.	0	0	0	0	0	0	4	0	1	0	0	0	0	0	1	2	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Rollieria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp.	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0
Grammatodon (Cosmetodon) sp.	0	0	0	2	0	2	2	0	0	0	0	3	2	1	0	0	0	0	0
Barbatia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. A	0	0	0	0	0	5	1	3	1	1	1	5	1	2	0	2	0	0	0
Isoarca sp. B	1	4	0	3	5	4	9	0	2	1	0	11	3	1	0	0	0	0	6
Isoarca sp. C	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Meleagrinella sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoceramid	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pinna sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Radulopecten strictus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spondylopecten sp.	3	4	0	3	19	8	4	0	2	3	0	3	2	0	1	2	0	2	3
Chlamys (Chlamys) textoria	0	0	0	0	0	0	1	2	0	1	0	0	0	0	0	0	0	1	0
Camptonectes (Camptonectes) auritus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (E.) nummulare	7	3	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (E.) corneolum	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	2
Entolium (Cingentolium) sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	4	0
Plagiostoma sp. E	1	1	0	0	1	4	1	0	1	0	0	0	0	0	0	0	0	0	1
Pseudolimea sp.	2	0	0	0	1	2	0	0	0	0	0	6	1	0	1	3	0	0	0
Aulacomyella sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acesta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Atreta sp.	3	0	3	5	6	0	4	0	1	4	4	0	0	0	0	1	0	0	0
Plicatula sp.	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	2	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon erucum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	0	3	0	0	0	0	8	1	0	0	0	0	0	0	0	0	0	0
Nanogyra nana	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Exogyra wetzleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liostrea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lucinid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Trigonia (Trigonia) sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella sp.	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pachyopsis sp.	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	7	0	0	1
Arcticid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astartid indet	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0
Protocardia (Protocardia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Anisocardia sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Integricardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia depressa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont indet	2	0	0	0	0	2	3	0	0	0	0	0	3	1	0	0	0	0	0
Pholadomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachymya (Arcomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 – Absolute abundances of brachiopods and bivalves.

	HW1-	RE3	RE5	HE2.1	HE2.2	HE7	HE5.1	HE5.2	LS1	LS2	GO16	LU1-1	LU1-5	LU1-7	LU1-9	LU2	LU3	LA1	LA2
Torquirhynchia speciosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella trilobata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella multiplicata	0	3	0	8	8	1	16	4	11	11	0	0	0	0	0	0	0	14	8
Lacunosella cracoviensis	0	3	0	9	10	0	8	0	0	0	3	0	0	0	0	0	0	0	0
Lacunosella pseudodecorata	0	26	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1
Lacunosella sparsicosta	0	0	0	0	0	0	0	0	0	0	0	0	14	28	0	6	24	91	30
Lacunosella polita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella striocincta	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0
Monticlarella czenstochaviensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella strioplicata	0	1	0	0	0	1	0	0	0	0	5	0	3	0	1	1	1	0	0
Monticlarella triloboides	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
Juralina insignis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argovithyris bisuffarcinata	0	0	0	0	0	0	0	2	0	0	0	0	1	1	1	3	1	0	0
Placothyris rollieri	0	6	14	0	0	0	0	0	24	15	19	0	0	0	0	0	0	0	0
Loboidothyris zieteni	0	0	0	44	65	50	49	25	0	0	0	42	26	57	34	17	23	54	21
Loboidothyris foraminata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucleata nucleata	0	10	0	0	0	0	0	1	0	0	0	6	7	7	0	0	3	22	16
Trigonellina loricata	0	0	0	1	0	1	0	0	1	0	2	0	0	0	0	0	0	0	0
Trigonellina pectunculus	0	1	0	0	0	0	0	0	0	0	0	2	4	2	0	0	1	0	0
Dictyothyris kurri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebratulina substriata	1	0	0	11	1	2	1	3	0	0	0	0	2	0	1	1	2	0	0
Ismenia pectunculoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina orbis	0	1	0	0	0	0	0	0	2	7	5	0	0	0	0	0	5	0	0
Zittelina gutta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina trisignata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria humeralis	0	0	0	0	0	0	0	0	0	0	0	10	11	6	3	0	0	0	0
Aulacothyris impressula	36	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0
Aulacothyris impressa	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Tegulithyris sp.	0	0	0	0	0	0	0	0	0	0	0	4	8	1	1	0	0	1	1
Ornithella lampas	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rollieria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Grammatodon (Grammatodon) sp.	2	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0
Grammatodon (Cosmetodon) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Barbatia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. A	0	0	1	0	0	2	3	3	0	0	2	8	0	0	0	3	3	0	1
Isoarca sp. B	0	1	0	0	0	0	0	1	1	1	2	0	0	0	0	0	0	1	4
Isoarca sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meleagrinella sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Inoceramid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Radulopecten strictus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spondylopecten sp.	0	0	0	0	0	0	0	0	3	2	0	1	0	1	0	0	0	1	0
Chlamys (Chlamys) textoria	1	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0
Camptonectes (Camptonectes) auritus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (E.) nummulare	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (E.) corneolum	4	1	1	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
Entolium (Cingentolium) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. E	0	0	1	0	0	0	3	0	0	1	3	1	0	0	1	0	0	0	1
Pseudolimea sp.	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0
Aulacomyella sp.	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acesta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atreta sp.	1	0	0	0	1	7	0	1	0	0	0	0	5	0	1	0	1	23	5
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Actinostreon erucum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	2	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Nanogyra nana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Exogyra wetzleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liostrea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lucinid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella sp.	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Pachyopsis sp.	0	5	2	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	7
Arcticid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Astartid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Anisocardia sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Integricardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia depressa	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Heterodont indet	3	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0
Pholadomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachymya (Arcomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) – Absolute abundances of brachiopods and bivalves.

	LA3-1	LA3-2	LA3-3	LA4	LA5	LU13.	UR1-0	UR1-1	UR1-2	UR1-4	UR1-6	GE1	GE2	GE3	GE4	GE5	GE6	GE7	GE8
Torquirhynchia speciosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella trilobata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella multiplicata	13	7	4	12	10	1	0	10	4	4	8	22	24	0	1	1	0	0	28
Lacunosella cracoviensis	4	0	0	0	0	0	27	0	0	90	0	0	0	0	0	0	0	0	0
Lacunosella pseudodecorata	18	9	6	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella sparsicosta	108	66	73	15	47	0	4	0	123	0	54	0	68	64	3	55	22	7	0
Lacunosella polita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella striocincta	0	0	0	0	0	0	4	4	0	2	0	16	12	12	0	0	3	8	13
Monticlarella czenstochaviensis	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Monticlarella strioplicata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Monticlarella triloboides	0	0	0	0	0	2	0	0	5	8	8	37	41	0	5	51	23	3	21
Juralina insignis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argovithyris bisuffarcinata	0	0	0	0	0	2	1	0	6	1	5	0	7	9	0	18	1	0	0
Placothyris rollieri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Loboidothyris zieteni	19	17	10	4	9	55	4	5	14	16	8	8	11	14	6	0	5	2	3
Loboidothyris foraminata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucleata nucleata	11	7	18	9	4	14	1	0	0	0	1	3	1	4	0	6	1	0	0
Trigonellina loricata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonellina pectunculus	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Dictyothyris kurri	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Terebratulina substriata	1	0	0	0	0	0	2	0	2	3	0	7	2	2	1	0	4	8	2
Ismenia pectunculoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina orbis	0	0	0	0	0	0	0	2	0	0	0	36	31	5	5	0	17	14	15
Zittelina gutta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina trisignata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria humeralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0
Aulacothyris impressula	0	0	0	0	0	2	2	0	5	7	2	10	1	1	0	17	0	4	0
Aulacothyris impressa	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tegulithyris sp.	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ornithella lampas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	1	1	0	0	1	2	0	0	0	0	0	3	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rollieria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Grammatodon (Grammatodon) sp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1
Grammatodon (Cosmetodon) sp.	4	1	2	0	0	0	0	1	0	0	1	4	0	2	0	2	0	0	1
Barbatia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. A	2	0	2	0	1	0	0	2	1	1	1	0	1	1	0	0	0	0	0
Isoarca sp. B	1	1	0	0	0	1	0	0	0	4	1	0	1	0	0	2	0	0	0
Isoarca sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Meleagrinella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoceramid	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0
Radulopecten strictus	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	0
Spondylopecten sp.	1	2	0	0	0	1	0	3	0	0	1	6	0	1	4	0	0	6	0
Chlamys (Chlamys) textoria	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	1
Camptonectes (Camptonectes) auritus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Entolium (E.) nummulare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (E.) corneolum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (Cingentolium) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma sp. E	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0
Pseudolimea sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Aulacomyella sp.	0	2	1	6	0	1	0	1	0	0	0	3	0	0	3	10	1	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Acesta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atreta sp.	24	13	9	0	8	0	0	0	10	4	7	0	8	2	0	3	0	0	0
Plicatula sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	2	1	0	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Actinostreon erucum	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0
Nanogyra nana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Exogyra wetzleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liostrea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lucinid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pachyopsis sp.	2	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0
Arcticid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Astartid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Anisocardia sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Integricardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Thracia depressa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Heterodont indet	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pholadomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachymya (Arcomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) – Absolute abundances of brachiopods and bivalves.

	GE9	GE10	GE11	GE12	GE17	GE18	GE19	GE20	GE22	HW5	HW8	HW9-	HWC	HWC2	HWD	HWE	HWF	GE13	GE14
Torquirhynchia speciosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella trilobata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella multiplicata	1	1	27	13	41	26	19	0	8	0	0	1	36	82	15	19	42	0	0
Lacunosella cracoviensis	0	0	0	16	11	0	12	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella pseudodecorata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella sparsicosta	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella polita	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella striocincta	2	13	0	0	4	0	0	0	1	0	0	0	2	1	5	0	2	0	0
Monticlarella czenstochaviensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella strioplicata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella triloboides	5	5	6	33	54	23	21	1	5	0	0	1	2	8	1	2	13	43	11
Juralina insignis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Argovithyris bisuffarcinata	3	3	0	1	6	1	3	0	1	0	0	0	0	0	0	0	0	0	0
Placothyris rollieri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Loboidothyris zieteni	0	0	6	30	0	3	4	0	0	2	0	0	2	9	2	5	8	9	6
Loboidothyris foraminata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucleata nucleata	0	0	3	0	5	0	3	0	3	0	0	1	0	2	2	2	3	14	2
Trigonellina loricata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonellina pectunculus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dictyothyris kurri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebratulina substriata	0	0	0	0	7	0	3	0	7	15	1	18	0	0	0	0	0	10	1
Ismenia pectunculoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina orbis	3	1	2	2	16	1	3	0	1	0	0	0	1	0	2	4	5	13	17
Zittelina gutta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina trisignata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria humeralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulacothyris impressula	0	0	0	2	3	0	1	0	0	11	9	21	0	3	0	0	0	0	0
Aulacothyris impressa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tegulithyris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ornithella lampas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	0	1	0	0	1	0	1	4	0	4	0	0	0	0	0	0	1
Palaeonucula sp.	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rollieria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp.	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0
Grammatodon (Cosmetodon) sp.	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Barbatia sp.	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. A	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. B	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meleagrinella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoceramid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Radulopecten strictus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spondylopecten sp.	2	0	1	0	3	1	1	0	1	1	0	0	0	2	0	0	0	0	1
Chlamys (Chlamys) textoria	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camptonectes (Camptonectes) auritus	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (E.) nummulare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (E.) corneolum	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0	0	1
Entolium (Cingentolium) sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3	0
Plagiostoma sp. E	2	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pseudolimea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Aulacomyella sp.	33	3	0	0	0	1	1	62	0	9	22	12	0	0	0	0	0	1	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acesta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atreta sp.	0	0	2	0	5	0	8	0	0	0	0	0	0	0	0	0	0	2	3
Plicatula sp.	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Placunopsis sp.	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Actinostreon erucum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nanogyra nana	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Exogyra wetzleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liostrea sp.	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
Lucinid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachyopsis sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcticid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astartid indet	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anisocardia sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Integricardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia depressa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont indet	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1
Pholadomya sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Pachymya (Arcomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 (cont.) – Absolute abundances of brachiopods and bivalves.

	GE15	GE16	GE21	UR2-1	UR2-3	UR2-5	UR2-6	UR2-8	UR2-9	AL1	AL2	AR1	AR2	AR3	SA1	SA3	SA4	SA5
Torquirhynchia speciosa	0	0	0	0	0	0	0	0	0	0	0	0	5	15	27	55	61	10
Lacunosella trilobata	0	0	0	0	0	0	0	0	0	1	6	0	0	0	0	0	0	0
Lacunosella multiplicata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella cracoviensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella pseudodecorata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella sparsicosta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella polita	0	0	0	21	35	277	51	72	5	0	0	0	0	0	0	0	0	0
Monticlarella striocincta	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Monticlarella czenstochaviensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella strioplicata	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Monticlarella triloboides	34	2	38	0	6	0	0	0	0	0	1	0	0	0	0	0	0	0
Juralina insignis	0	0	0	0	0	0	0	0	0	0	0	0	14	16	110	65	134	180
Argovithyris bisuffarcinata	0	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Placothyris rollieri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Loboidothyris zieteni	15	14	5	11	3	0	0	3	3	0	0	0	0	0	0	0	0	0
Loboidothyris foraminata	0	0	0	0	0	0	0	0	0	44	20	10	0	0	0	0	0	0
Nucleata nucleata	4	0	0	0	4	5	1	5	0	0	0	0	0	0	0	0	0	0
Trigonellina loricata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonellina pectunculus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dictyothyris kurri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Terebratulina substriata	5	0	1	1	0	1	0	0	0	0	0	0	0	0	0	3	0	1
Ismenia pectunculoides	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	11	5	1
Zittelina orbis	17	1	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina gutta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina trisignata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria humeralis	0	0	0	0	1	0	0	0	5	0	0	0	0	0	0	0	0	0
Aulacothyris impressula	0	0	0	0	5	24	2	35	54	0	0	0	0	0	0	0	0	0
Aulacothyris impressa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tegulithyris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ornithella lampas	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rollieria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Cosmetodon) sp.	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Barbatia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Isoarca sp. A	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Isoarca sp. B	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Isoarca sp. C	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Mytilus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meleagrinella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoceramid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0
Eopecten sp.	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	5	1
Radulopecten strictus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spondylopecten sp.	1	0	3	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Chlamys (Chlamys) textoria	3	0	0	0	0	0	0	0	0	4	4	14	0	1	1	0	1	2
Camptonectes (Camptonectes) auritus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Entolium (E.) nummulare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (E.) corneolum	0	0	0	0	0	0	0	0	0	0	1	4	0	0	2	1	2	0
Entolium (Cingentolium) sp.	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Plagiostoma sp. E	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0
Pseudolimea sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	2
Aulacomyella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acesta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atreta sp.	4	6	0	0	2	2	2	0	0	0	0	0	0	0	0	2	0	0
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	1	0	4	0	0	1	2	0	0
Actinostreon erucum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	0	0	0	0	0	0	0	0	0	0	3	3	3	1	3	1	1
Nanogyra nana	1	0	0	0	0	0	0	0	0	0	0	1	0	4	0	0	0	0
Exogyra wetzleri	0	0	0	0	0	0	0	0	0	0	0	0	2	3	4	10	3	0
Liostrea sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lucinid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pachyopsis sp.	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Arcticid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astartid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anisocardia sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Integricardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia depressa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachymya (Arcomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Supplement 1 (cont.) – Absolute abundances of brachiopods and bivalves.

Species	Guild
Torquirhynchia speciosa	pedunculate brachiopod
Lacunosella trilobata	pedunculate brachiopod
Lacunosella multiplicata	pedunculate brachiopod
Lacunosella subsimilis	pedunculate brachiopod
Lacunosella decorata	pedunculate brachiopod
Lacunosella sparsicosta	pedunculate brachiopod
Lacunosella aff. polita	pedunculate brachiopod
Monticlarella striocincta	pedunculate brachiopod
Monticlarella czenstochaviensis	pedunculate brachiopod
Monticlarella strioplicata	pedunculate brachiopod
Monticlarella triloboides	pedunculate brachiopod
Juralina insignis	pedunculate brachiopod
Argovithyris bisuffarcinata	pedunculate brachiopod
Placothyris rollieri	pedunculate brachiopod
Loboidothyris zieteni	pedunculate brachiopod
Loboidothyris gigas	pedunculate brachiopod
Loboidothyris foraminata	pedunculate brachiopod
Nucleata nucleata	pedunculate brachiopod
Trigonellina loricata	pedunculate brachiopod
Trigonellina pectunculus	pedunculate brachiopod
Dictyothyris kurri	pedunculate brachiopod
Terebratulina substriata	pedunculate brachiopod
Ismenia pectunculoides	pedunculate brachiopod
Zittelina orbis	pedunculate brachiopod
Zittelina gutta	pedunculate brachiopod
Zittelina trisignata	pedunculate brachiopod
Zeilleria humeralis	pedunculate brachiopod
Aulacothyris impressula	pedunculate brachiopod
Aulacothyris impressa	pedunculate brachiopod
Tegulithyris sp.	pedunculate brachiopod
Ornithella lampas	pedunculate brachiopod
Nuculoma sp.	shallow burrowing protobranch
Palaeonucula sp.	shallow burrowing protobranch
Mesosaccella sp.	shallow burrowing protobranch
Rollieria sp.	shallow burrowing protobranch
Grammatodon (Grammatodon) sp.	epibyssate filibranch
Grammatodon (Cosmetodon) sp.	endobyssate filibranch
Barbatia sp.	endobyssate filibranch
Isoarca sp. A	shallow burrowing protobranch
Isoarca sp. B	shallow burrowing protobranch
Isoarca sp. C	shallow burrowing protobranch
Arcomytilus sp.	epibyssate filibranch
Mytilus sp.	epibyssate filibranch
Modiolus sp.	endobyssate filibranch
Gervillella sp.	endobyssate filibranch
Oxytoma sp.	epibyssate filibranch
Meleagrinella sp.	epibyssate filibranch
Inoceramid	epibyssate filibranch
Pinna sp.	endobyssate filibranch
Ctenostreon sp.	epibyssate filibranch
Eopecten sp.	epibyssate filibranch
Radulopecten strictus	epibyssate filibranch
Spondylopecten sp.	epibyssate filibranch
Chlamys (Chlamys) textoria	epibyssate filibranch
Camptonectes (Camptonectes) auritus	epibyssate filibranch
Entolium (E.) nummulare	free-lying filibranch
Entolium (E.) corneolum	free-lying filibranch
Entolium (Cingentolium) sp.	free-lying filibranch
Plagiostoma sp. E	epibyssate filibranch
Pseudolimea sp.	epibyssate filibranch
Aulacomyella sp.	epibyssate filibranch
Limatula sp.	epibyssate filibranch
Acesta sp.	epibyssate filibranch
Atreta sp.	cementing filibranch
Plicatula sp.	cementing filibranch
Placunopsis sp.	cementing filibranch
Actinostreon erucum	cementing pseudolamellibranch
Actinostreon gregareum	cementing pseudolamellibranch
Nanogyra nana	cementing pseudolamellibranch
Exogyra wetzleri	cementing pseudolamellibranch
Liostrea sp.	cementing pseudolamellibranch
Lucinid indet	deep burrowing chemosymbiont
Trigonia (Trigonia) sp.	shallow burrowing filibranch
Nicaniella sp.	shallow burrowing eulamellibranch
Pachyopsis sp.	shallow burrowing eulamellibranch
Arcticid indet	shallow burrowing eulamellibranch
Astartid indet	shallow burrowing eulamellibranch
Protocardia (Protocardia) sp.	shallow burrowing eulamellibranch
Anisocardia sp. A	shallow burrowing eulamellibranch
Integricardium sp.	shallow burrowing eulamellibranch
Thracia depressa	deep burrowing eulamellibranch
Heterodont indet	shallow burrowing eulamellibranch
Pholadomya sp.	deep burrowing eulamellibranch
Pachymya (Arcomya) sp.	deep burrowing eulamellibranch

Supplement 2 – Assignments of brachiopods and bivalves to guilds.

Sample	Zone	Siliciclastic	Habitat	Consistency
LG1	*Dichotomoceras bifurcatum*	marlstone	Below MSWB	mixed-bottom
LG2	*Dichotomoceras bifurcatum*	marlstone	Below MSWB	mixed-bottom
LG3	*Dichotomoceras bifurcatum*	marlstone	Above MSWB	mixed-bottom
SM1	*Dichotomoceras bifurcatum*	marlstone	Above MSWB	mixed-bottom
SM2	*Dichotomoceras bifurcatum*	marlstone	Above MSWB	mixed-bottom
GO1	*Epipeltoceras bimammatum*	marly limestone	Above MSWB	hard-bottom
GO2	*Epipeltoceras bimammatum*	marlstone	Above MSWB	mixed-bottom
GO3	*Epipeltoceras bimammatum*	marly limestone	Above MSWB	hard-bottom
GO4	*Epipeltoceras bimammatum*	marlstone	Above MSWB	hard-bottom
GO5	*Epipeltoceras bimammatum*	marly limestone	Above MSWB	hard-bottom
GO6	*Epipeltoceras bimammatum*	marly limestone	Above MSWB	hard-bottom
GO7	*Epipeltoceras bimammatum*	marlstone	Above MSWB	hard-bottom
GO9	*Epipeltoceras bimammatum*	marlstone	Above MSWB	mixed-bottom
GO10	*Epipeltoceras bimammatum*	limestone	Above MSWB	hard-bottom
GO11	*Epipeltoceras bimammatum*	marly limestone	Above MSWB	hard-bottom
GO12	*Epipeltoceras bimammatum*	marly limestone	Above MSWB	hard-bottom
GO13	*Epipeltoceras bimammatum*	marly limestone	Above MSWB	hard-bottom
GO14	*Epipeltoceras bimammatum*	marlstone	Above MSWB	mixed-bottom
GO15	*Epipeltoceras bimammatum*	marlstone	Above MSWB	mixed-bottom
HW1-2	*Epipeltoceras bimammatum*	marlstone	Below MSWB	mixed-bottom
RE3	*Subnebrodites planula*	limestone	Above MSWB	mixed-bottom
RE5	*Subnebrodites planula*	limestone	Above MSWB	mixed-bottom
HE2.1	*Subnebrodites planula*	marly limestone	Above MSWB	hard-bottom
HE2.2	*Subnebrodites planula*	marly limestone	Above MSWB	hard-bottom
HE7	*Subnebrodites planula*	marly limestone	Above MSWB	hard-bottom
HE5.1	*Subnebrodites planula*	marly limestone	Above MSWB	hard-bottom
HE5.2	*Subnebrodites planula*	marly limestone	Above MSWB	hard-bottom
LS1	*Subnebrodites planula*	limestone	Above MSWB	hard-bottom
LS2	*Subnebrodites planula*	limestone	Above MSWB	hard-bottom
GO16	*Subnebrodites planula*	limestone	Above MSWB	mixed-bottom
LU1-1	*Sutneria platynota*	marlstone	Below MSWB	hard-bottom
LU1-5	*Sutneria platynota*	marlstone	Below MSWB	hard-bottom
LU1-7	*Sutneria platynota*	marlstone	Below MSWB	hard-bottom
LU1-9	*Sutneria platynota*	marlstone	Below MSWB	hard-bottom
LU2	*Sutneria platynota*	marlstone	Below MSWB	hard-bottom
LU3	*Sutneria platynota*	marlstone	Below MSWB	hard-bottom
LA1	*Sutneria platynota*	marly limestone	Above MSWB	hard-bottom
LA2	*Sutneria platynota*	marly limestone	Above MSWB	hard-bottom
LA3-1	*Sutneria platynota*	marly limestone	Above MSWB	hard-bottom
LA3-2	*Sutneria platynota*	marly limestone	Above MSWB	hard-bottom
LA3-3	*Sutneria platynota*	marly limestone	Above MSWB	hard-bottom
LA4	*Sutneria platynota*	limestone	Above MSWB	hard-bottom
LA5	*Sutneria platynota*	marly limestone	Above MSWB	hard-bottom
LU13.4	*Ataxioceras hypselocyclum*	limestone	Above MSWB	hard-bottom
UR1-0	*Ataxioceras hypselocyclum*	limestone	Below MSWB	hard-bottom
UR1-1	*Ataxioceras hypselocyclum*	limestone	Below MSWB	hard-bottom
UR1-2	*Ataxioceras hypselocyclum*	limestone	Below MSWB	hard-bottom
UR1-4	*Ataxioceras hypselocyclum*	limestone	Below MSWB	hard-bottom
UR1-6	*Ataxioceras hypselocyclum*	marly limestone	Below MSWB	hard-bottom
GE1	*Ataxioceras hypselocyclum*	marlstone	Above MSWB	mixed-bottom
GE2	*Ataxioceras hypselocyclum*	marly limestone	Above MSWB	hard-bottom
GE3	*Ataxioceras hypselocyclum*	marly limestone	Above MSWB	hard-bottom
GE4	*Ataxioceras hypselocyclum*	marlstone	Above MSWB	mixed-bottom
GE5	*Ataxioceras hypselocyclum*	marly limestone	Above MSWB	hard-bottom
GE6	*Ataxioceras hypselocyclum*	marly limestone	Above MSWB	hard-bottom
GE7	*Ataxioceras hypselocyclum*	marly limestone	Above MSWB	mixed-bottom
GE8	*Ataxioceras hypselocyclum*	marly limestone	Above MSWB	hard-bottom
GE9	*Ataxioceras hypselocyclum*	marlstone	Above MSWB	mixed-bottom
GE10	*Ataxioceras hypselocyclum*	marlstone	Above MSWB	mixed-bottom
GE11	*Ataxioceras hypselocyclum*	limestone	Above MSWB	hard-bottom
GE12	*Ataxioceras hypselocyclum*	marly limestone	Above MSWB	hard-bottom

Supplement 3 – Environmental and stratigraphic assignments.

Sample	Zone	Siliciclastic	Habitat	Consistency
GE17	*Ataxioceras hypselocyclum*	marlstone	Above MSWB	hard-bottom
GE18	*Ataxioceras hypselocyclum*	marly limestone	Above MSWB	hard-bottom
GE19	*Ataxioceras hypselocyclum*	marlstone	Above MSWB	hard-bottom
GE20	*Ataxioceras hypselocyclum*	marlstone	Above MSWB	mixed-bottom
GE22	*Ataxioceras hypselocyclum*	marly limestone	Below MSWB	mixed-bottom
HW5	*Ataxioceras hypselocyclum*	marlstone	Below MSWB	mixed-bottom
HW8	*Ataxioceras hypselocyclum*	marlstone	Below MSWB	mixed-bottom
HW9-10	*Ataxioceras hypselocyclum*	marlstone	Above MSWB	mixed-bottom
HWC1	*Ataxioceras hypselocyclum*	limestone	Above MSWB	hard-bottom
HWC2	*Ataxioceras hypselocyclum*	limestone	Above MSWB	hard-bottom
HWD	*Ataxioceras hypselocyclum*	limestone	Above MSWB	hard-bottom
HWE	*Ataxioceras hypselocyclum*	limestone	Above MSWB	hard-bottom
HWF	*Ataxioceras hypselocyclum*	limestone	Above MSWB	hard-bottom
GE13	*Crussoliceras divisum*	marlstone	Above MSWB	mixed-bottom
GE14	*Crussoliceras divisum*	marlstone	Above MSWB	mixed-bottom
GE15	*Crussoliceras divisum*	marlstone	Above MSWB	mixed-bottom
GE16	*Crussoliceras divisum*	marly limestone	Above MSWB	hard-bottom
GE21	*Crussoliceras divisum*	marlstone	Below MSWB	hard-bottom
UR2-1	*Aulacostephanus mutabilis*	limestone	Above MSWB	hard-bottom
UR2-3	*Aulacostephanus mutabilis*	marly limestone	Above NSWB	mixed-bottom
UR2-5	*Aulacostephanus mutabilis*	marly limestone	Above MSWB	hard-bottom
UR2-6	*Aulacostephanus mutabilis*	marly limestone	Above MSWB	hard-bottom
UR2-8	*Aulacostephanus mutabilis*	marly limestone	Above MSWB	mixed-bottom
UR2-9	*Aulacostephanus mutabilis*	marly limestone	Above MSWB	mixed-bottom
AL1	*Hybonoticeras beckeri*	limestone	Above MSWB	hard-bottom
AL2	*Hybonoticeras beckeri*	limestone	Above NSWB	hard-bottom
AR1	*Hybonoticeras beckeri*	limestone	Above NSWB	hard-bottom
AR2	*Hybonoticeras beckeri*	limestone	Above FWWB	skeletal sand
AR3	*Hybonoticeras beckeri*	limestone	Above FWWB	skeletal sand
SA1	*Hybonoticeras beckeri*	limestone	Above FWWB	skeletal sand
SA3	*Hybonoticeras beckeri*	limestone	Above FWWB	skeletal sand
SA4	*Hybonoticeras beckeri*	limestone	Above FWWB	skeletal sand
SA5	*Hybonoticeras beckeri*	limestone	Above FWWB	skeletal sand

Supplement 3 (cont.) - Environmental and stratigraphic assignments.

11. Ecology of brachiopods and bivalves in the Oxfordian of the Swiss Jura

(with Franz T. Fürsich)

Abstract. The Oxfordian deposits of the Swiss Jura represent a transition between a shallow carbonate platform and a deep epicontinental shelf. They contain benthic communities that partly contrast with sponge-dominated benthic communities with brachiopods that were typical of epicontinental seas in southern Germany. During the Early and early Middle Oxfordian, infaunal bivalves dominated in soft-bottom, terrigenous-rich habitats, and epibyssate and cementing bivalves were most abundant in hard-bottom, carbonate-rich habitats with corals. Brachiopod species were common both in soft-bottom and hard-bottom habitats that markedly differed in the siliciclastic supply. This implies pronounced tolerance of brachiopods with respect to varying siliciclastic supply, with the rhynchonellid *Thurmanella* being especially well adapted to siliciclastic-rich, soft-bottom habitats. During the Late Oxfordian characterized by carbonate deposition and reduced siliciclastic supply, cementing bivalves and brachiopods dominated in shallow, mixed-bottom habitats on the platform, and infaunal bivalves were abundant in deep-shelf, soft-bottom habitats. Abundance of infaunal bivalves in offshore, carbonate-rich deposits of the Swiss Jura contrasts with their rarity in co-eval offshore, soft-bottom habitats of southern Germany. Rarity of infaunal bivalves in the Swabian-Franconian epicontinental sea during Late Oxfordian was not probably owing to the scarcity of land-derived nutrients because this region was similarly close or closer to siliciclastic sources of the Rhenish Massif as the Swiss Jura Platform. Instead, the high abundance of infaunal bivalves in the Swiss Jura can be more related to well aerated bottom conditions near platform margin, in contrast to *Chondrites*-rich marls and limestones of southern Germany that probably originated under reduced flow velocity and reduced oxygen levels.

Introduction

In this chapter, benthic communities that inhabited relatively shallow, mixed, siliciclastic-carbonate environments of the Swiss Jura (Fig. 1) during the Oxfordian are described and analyzed. They were temporally equivalent to extensive sponge-dominated communities of deeper epicontinental seas of the northern Tethys shelf. Such communities occurred in southern Portugal, SE Spain, SE France, Switzerland, southern Germany, Poland and Rumania during Late Jurassic (Keupp et al., 1990; Leinfelder et al., 2002). Sponge communities were colonized by abundant and relatively diverse brachiopods that commonly dominated in terms of numerical abundance among other level-bottom fauna. The success of brachiopods in such communities belongs to unresolved ecologic puzzles and its causes should be relevant for understanding their evolutionary and ecologic history. The sponge-dominated communities from the Upper Jurassic have rather poor present-day counterparts and understanding their ecology thus depends mainly on quantitative analyses of fossil communities. Tracing variations in community composition along an onshore-offshore gradient from deeper shelf to platform might provide one of the tools that can enlighten environmental preferences and unique character of the Late Jurassic benthic communities of the northern Tethys shelf. The Swiss Jura platform is suitable for temporally restricted ecologic analyses owing to well-known and detailed ammonite-based biostratigraphic analyses (Gygi, 2000a). In this study, onshore-offshore gradient is evaluated in two time slices, including (1) Early Oxfordian – early Middle Oxfordian (*Cardioceras cordatum* Zone and the lower part of the *Gregoryceras transversarium* Zone), and (2) Late Oxfordian

(*Epipeltoceras bimammatum* Zone). The first time slice temporally precedes the onset of sponge communities in southern Germany and NE Switzerland that correspons to the upper part of the *G. transversarium* Zone. An evaluation of benthic faunas from the second time slice should provide information about composition of onshore communities that graded towards NE into offshore sponge-rich communities.

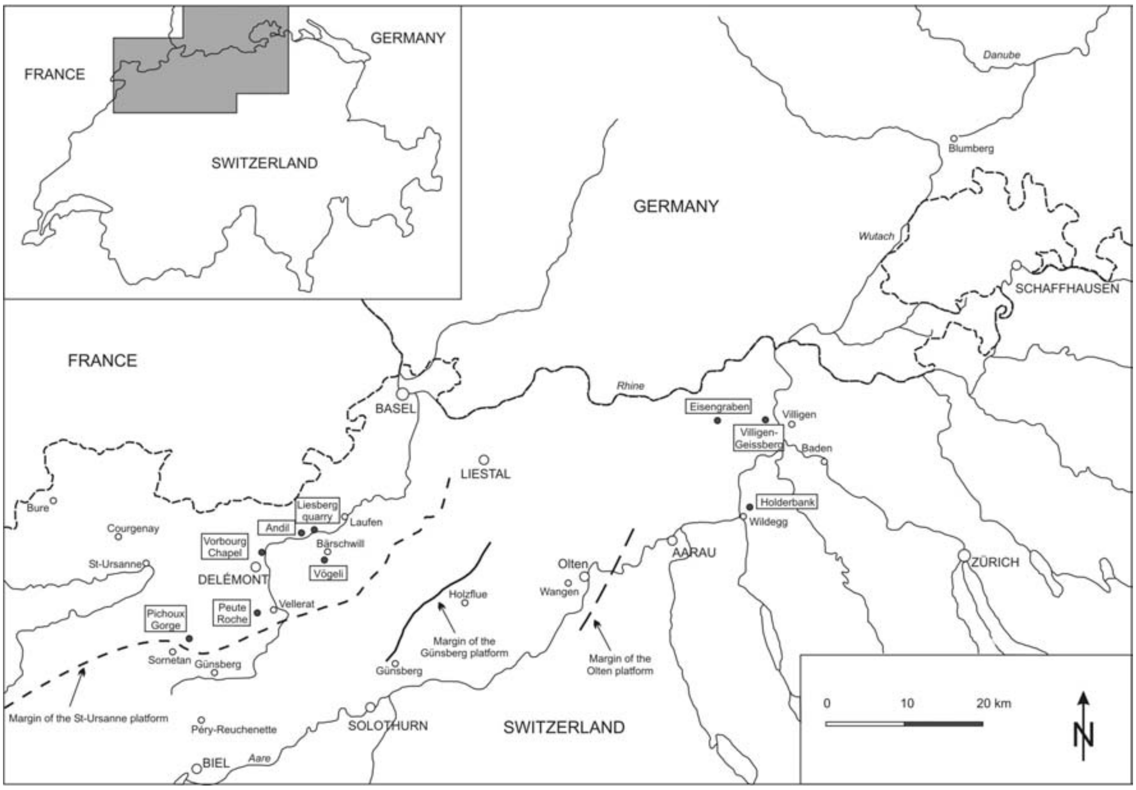


Figure 1 - Geographic location of nine sections in the Swiss Jura (modified according to Gygi, 2000a).

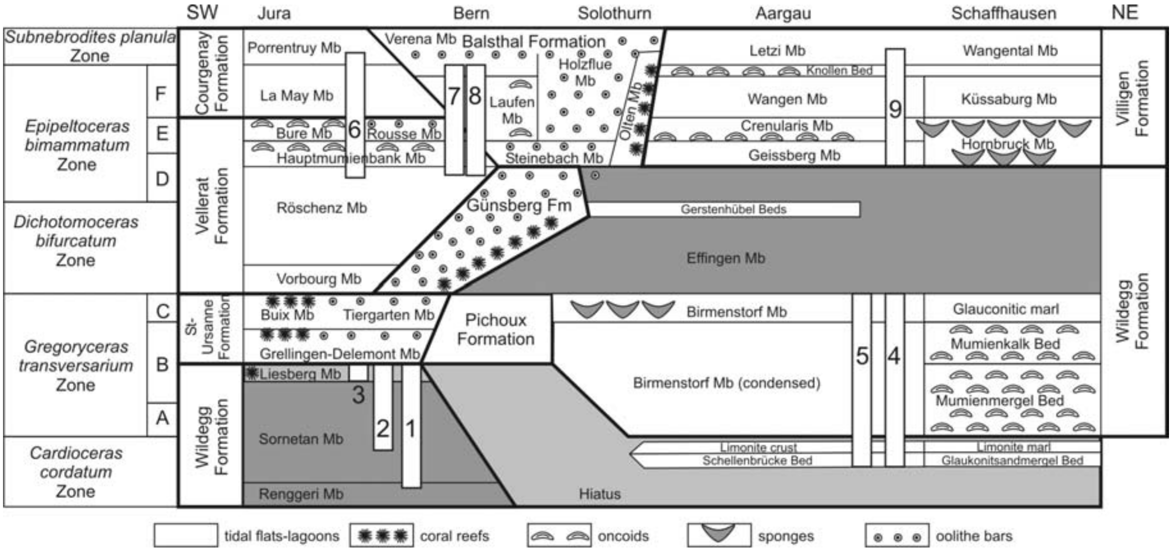


Figure 2 - Oxfordian – lowermost Kimmeridgian lithostratigraphic formations in the Swiss Jura across a simplified, SW-NE oriented onshore-offshore transect (modified according to Gygi, 2000a). The schematic position of nine sections is shown. 1 – Liesberg-Andil, 2 – Bärschwill-Vögeli, 3 – Peute Roche, 4 – Eisengraben, 5 – Holderbank, 6 - Vorbourg Chapel, 7 – Pichoux Gorge, 8 – Liesberg quarry, 9 – Villigen-Geissberg. A – *Cardioceras densipliatum* Subzone, B – *Perisphinctes antecedens* Subzone, C – *Perisphinctes luciaeformis* Subzone, D – *Euaspidoceras hypselum* Subzone, E – *Epipeltoceras bimammatum* Subzone, F. *Taramelliceras hauffianum* Subzone.

Setting

During the Late Jurassic, a mixed, carbonate-siliciclastic platform in the western part and an epicontinental basin in the eastern part of the Swiss Jura belonged to the northern shelf of the Tethys ocean in the subtropical climatic belt (Gygi, 1990a). In NE direction, this depositional area passed into an epicontinental basin of southern Germany that was differentiated into the Swabian Basin and the Franconian Platform (Meyer and Schmid-Kaler, 1990). The depositional area of the Swiss Jura was affected by varying rates of siliciclastic supply and carbonate production during the Oxfordian (Gygi and Persoz, 1986; Pittet and Strasser, 1998a). In addition, the sea-floor differentiation into swells and depressions was partly inherited from the pre-Jurassic basement and the sea-floor topography was also strongly influenced by synsedimentary tectonics that led to relief reversals during the Oxfordian (Allenbach, 2001). During the Early - early Middle Oxfordian, high rate of siliciclastic supply characterized the Bärschwill Basin in the northwestern parts of the Swiss Jura (Gygi, 1986). In contrast, during the upper Middle Oxfordian, the siliciclastic sediments were trapped mainly in the Effingen Basin in the eastern part of the Swiss Jura (Allenbach, 2002). During the Late Oxfordian (*Epipeltoceras bimammatum* Zone), carbonate-rich sedimentation with temporal sedimentation breaks prevailed and siliciclastic supply was reduced. In this time, the platform-epicontinental basin transition was characterized by a distinct zonation represented by the shallowest peritidal environments in the western part, followed by shallow lagoons with oncoids, oolite bars and rimming coral reefs in the eastern part of the Swiss Jura Platform (Gygi and Persoz, 1987). Three main phases of basinward progradation of oolite bars and coral reefs took place during the Oxfordian in the Swiss Jura (Gygi, 1986; Gygi and Persoz, 1986), including progradation of the St-Ursanne Formation (upper part of the *Gregoryceras transversarium* Zone), progradation of the Günsberg Formation (upper part of the *Dichotomoceras bifurcatus* Zone), and progradation of the Olten Formation (upper part of the *Epipeltoceras bimammatum* Zone).

Sections

Nine sections were sampled in the Swiss Jura (Fig. 2). Three section correspond to the Lower and the lower part of the Middle Oxfordian (Bärschwill Formation), two sections to the upper part of the Middle Oxfordian (Wildegg Formation), and four sections to the Upper Oxfordian (Vellerat, Balsthal, and Villigen formations).

Lower-lower Middle Oxfordian (Bärschwill Formation)

(1) Liesberg-clay pit of Andil. It exposes an about 90 m-thick, Lower-Middle Oxfordian succession of the Bärschwill Formation. This formation consists of the Renggeri, Sornetan and Liesberg members. The Renggeri Member is formed by a homogeneous marl with pyritized ammonites and rare benthic fauna (*C. cordatum* Zone, Gygi, 1990b). The Sornetan Member (equivalent to the Terrain à Chailles Member) consists of a rhythmic alternation of dark grey, organic-rich silty marls with light grey marly limestones (Fig. 3). Towards the upper parts, the proportion of silty admixture is decreasing and the member is formed by alternation of marls with marly limestones. Lithified marlstone and marly limestone beds have commonly irregular bedding planes and some carbonate-rich levels are represented by bands of limestone concretions. Marls commonly contain

pyritized burrows. The deposits contain ammonites and some levels ara characterized by abundance of the pedunculate brachiopods *Thurmanella obtrita* and *Galliennithyris galliennei*, bivalves and echinoids. The proportion of bioclasts gradually increases towards the upper parts of the Sornetan Member. An about 45 m-thick part of the Sornetan Member belongs to the *C. cordatum* Zone and an about 20 m-thick part belongs to the *G. transversarium* Zone. This member is overlain by dark shell-rich marls and marly floatstones and framestones of the Liesberg Member (Fig. 3, *G. transversarium* Zone) with in situ platy corals and abundant crinoids, echinoids, calcareous sponges, bivalves, brachiopods and serpulids. Bioclasts in the Liesberg Member are heavily bored and encrusted. Tops of platy corals are commonly covered with aggregations of the cementing oyster *Liostrea* sp. and serpulids. The exposure of the Liesberg Member in the Andil clay pit attains about 15 meters in thickness.

(2) Bärschwill-Vogeli. A natural outcrop formed by the landslide W of the Vögeli farm near Bärschwill is exposing an about 22 m-thick succession of the Sornetan Member and a 15 m-thick succession of the Liesberg Member (Gygi, 2000a). The Sornetan Member consists of silty marls and concretionary marly limestones, locally with common bivalves (*Protocardia (P.)* sp., *Entolium [E.] corneolum*) and brachiopods (*Thurmanella obtrita*). The boundary between the Sornetan and Liesberg members is gradual, formed by bioclastic-rich marls and limestones with platy corals, crinoids and serpulids (Fig. 4). The Liesberg Member consists of 5 to 10 cm-thick coral framestones and floatstones that alternate with thin, marly, bioclastic-rich layers (Fig. 4). The base of the St-Ursanne Formation is formed by 50 to 100 cm-thick coral framestones of the Grellingen Member.

(3) Peute Roche. A 12 m-thick Liesberg Member is presently exposed in the lower parts of Peute Roche cliff 1 km SW of Vellerat. Gygi (2000a) described an about 140 m-thick section through this cliff with the Bärschwill and St-Ursanne formations. Presently, the Sornetan Member is poorly exposed. The Liesberg Member is approximately 15 m-thick and consists of 10 to 20 cm-thick bioclastic marls and marly limestones with corals, serpulids and crinoids in the lower parts, and thick-bedded coral floatstones and framestones with beds and lenses of well sorted calcarenitic packstones in the upper parts (Fig. 5). The Liesberg Member gradually passess into massive coral framestones of the Grellingen Member that forms the cliff walls.

upper Middle Oxfordian (Wildegg Formation)

(4) Eisengraben. Small outcrops 1.5 km NW of the Mönthal village, NW of Brugg in the Aargau Canton expose an about 6 meters thick Birmenstorf Member of the Wildegg Formation (Gygi, 1969, Boullier, 1976). In this section the Birmenstorf Member overlies crinoidal limestones of the Callovian and a 30 cm-thick limestone interval with ferrigenous ooids of the Lower Oxfordian (*Cardioceras cordatum* Zone, Gygi, 1966, 1969, 1977). The Birmenstorf Member consists of dm-scale marly sponge boundstones with common microbial crusts that alternate with sponge-rich marls with rare microbial crusts (Fig. 6). Limestones and marls contain abundant ammonites and brachiopods. Macrobenthic communities are dominated by the terebratulid *Argovithyris birmensdorfensis*. Marls and the lower parts of limestones may also contain the abundant trace fossil *Chondrites*. The lowermost bed of the Birmenstorf Member is highly condensed in the Swiss Jura and represents the upper part of the *Cardioceras densiplicatum* Subzone and the *Perisphinctes antecedens* Subzone. The main part of this member thus belongs to the upper part of the *G. transversarium* Zone (*Perisphinctes luciaeformis* Subzone).

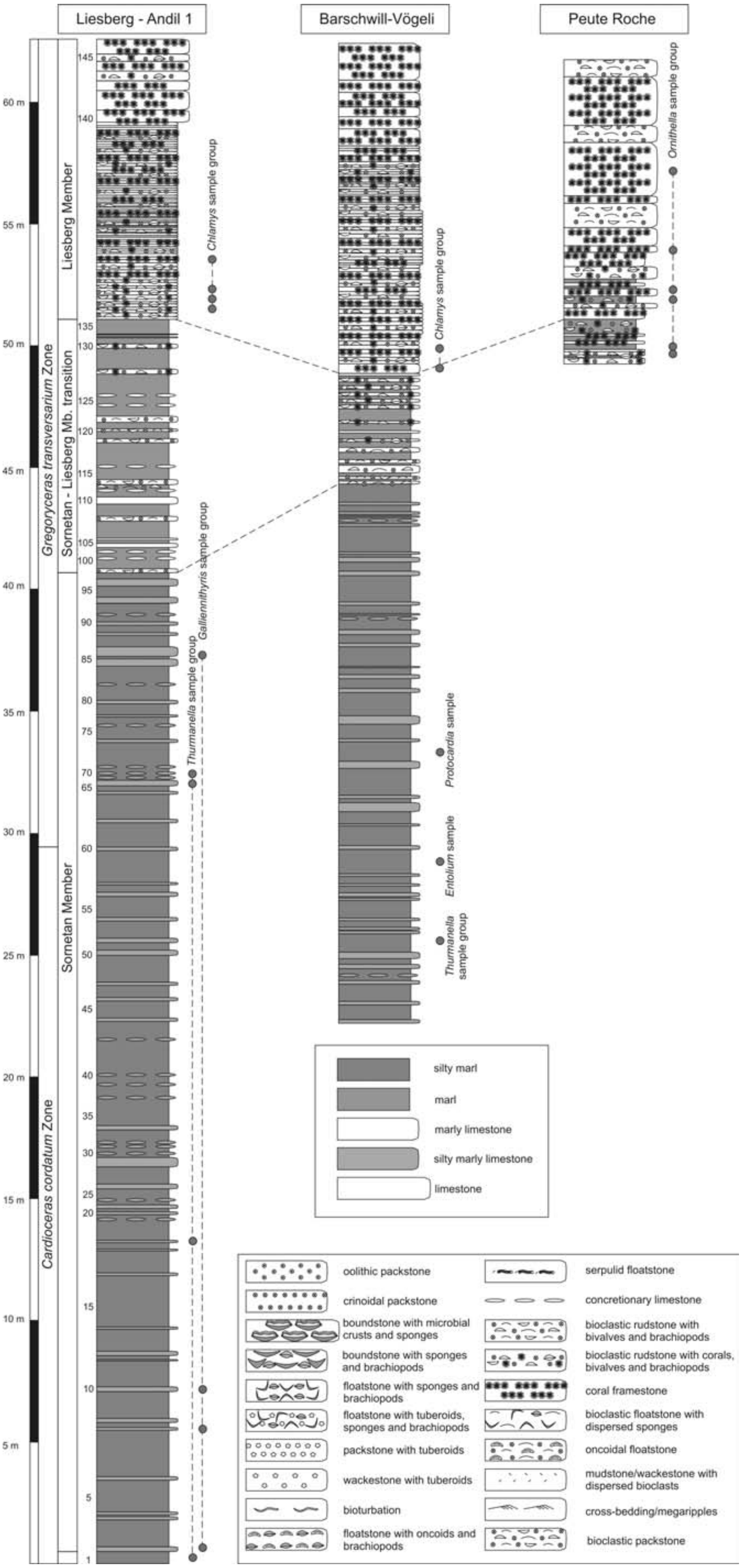


Figure 3 - Stratigraphic distribution of sample groups in three sections with the Lower – lower Middle Oxfordian deposits of the Bärschwill Formation.

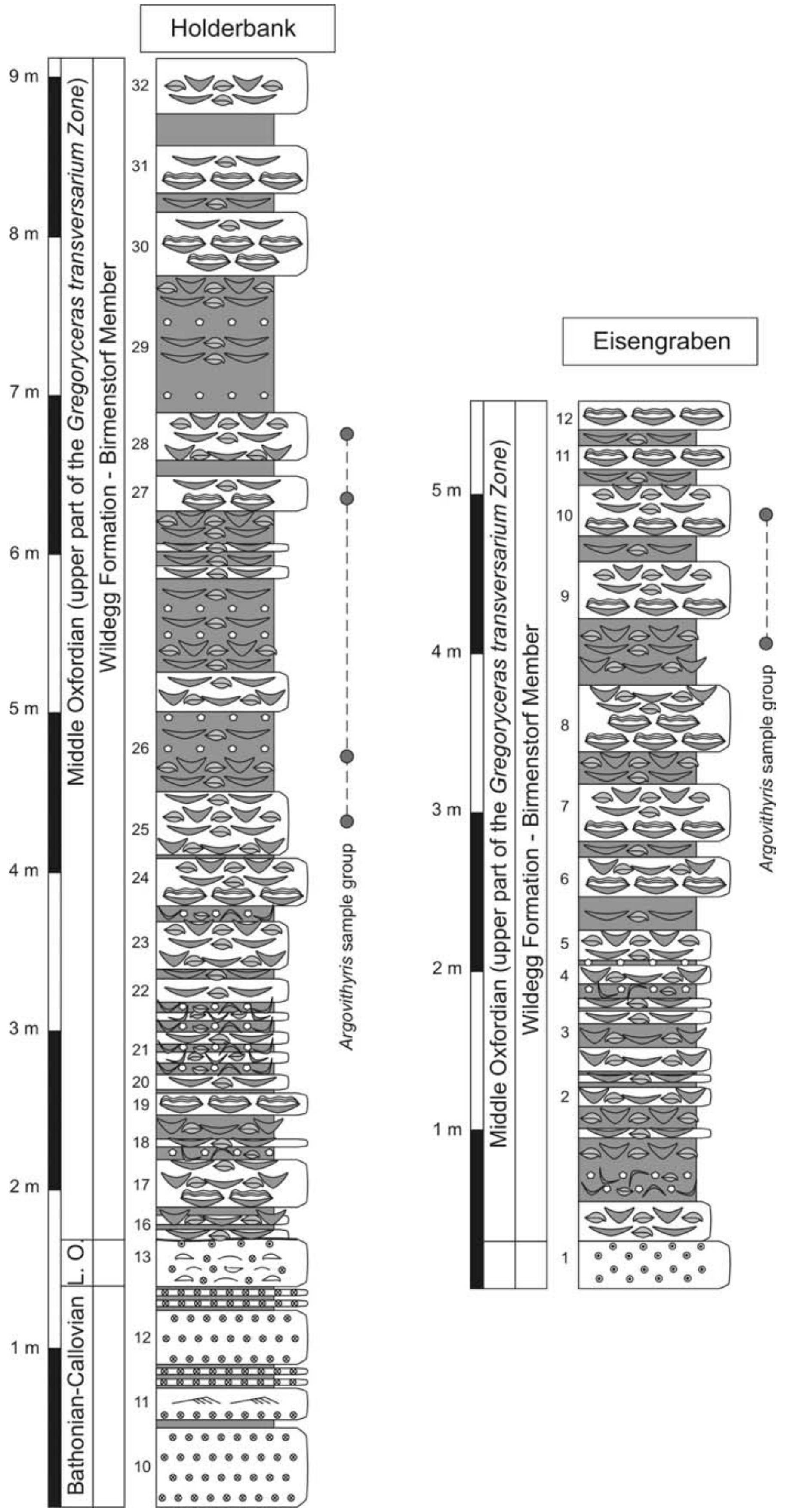


Figure 4 - Stratigraphic distribution of sample groups in two sections with upper Middle Oxfordian deposits of the Wildegg Formation. Explanations: Fig. 3.

(5) Holderbank. The section exposing the Callovian-Oxfordian deposits is situated in an old quarry 500 m NE of Holderbank, SW of Brugg in the Aargau Canton (Gygi et al., 1979; Kugler, 1987). Well sorted and densely packed, cross bedded crinoidal limestones with brachiopod and bivalve debris of the Bathonian-Callovian are overlain by a 30 cm-thick, highly condensed bioclastic-intraclastic packstone with Fe-crusts (Schnellenbrücke Bed, Lower Oxfordian, *Cardioceras cordatum* Zone). The lowermost, 1.7 m-thick part of the Birmenstorf Member consists of sponge boundstones and sponge-rich marls that are enriched in glauconite and contain very rare brachiopods and bivalves. Benthic macrofauna is more abundant in the middle and upper parts of the Birmenstorf Member that contains also several thick marls with tuberoids, *Chondrites* and dispersed or loose sponges (Fig. 7). This member is overlain by the terrigenous-rich Effingen Member (*D. bifurcatus* Zone).

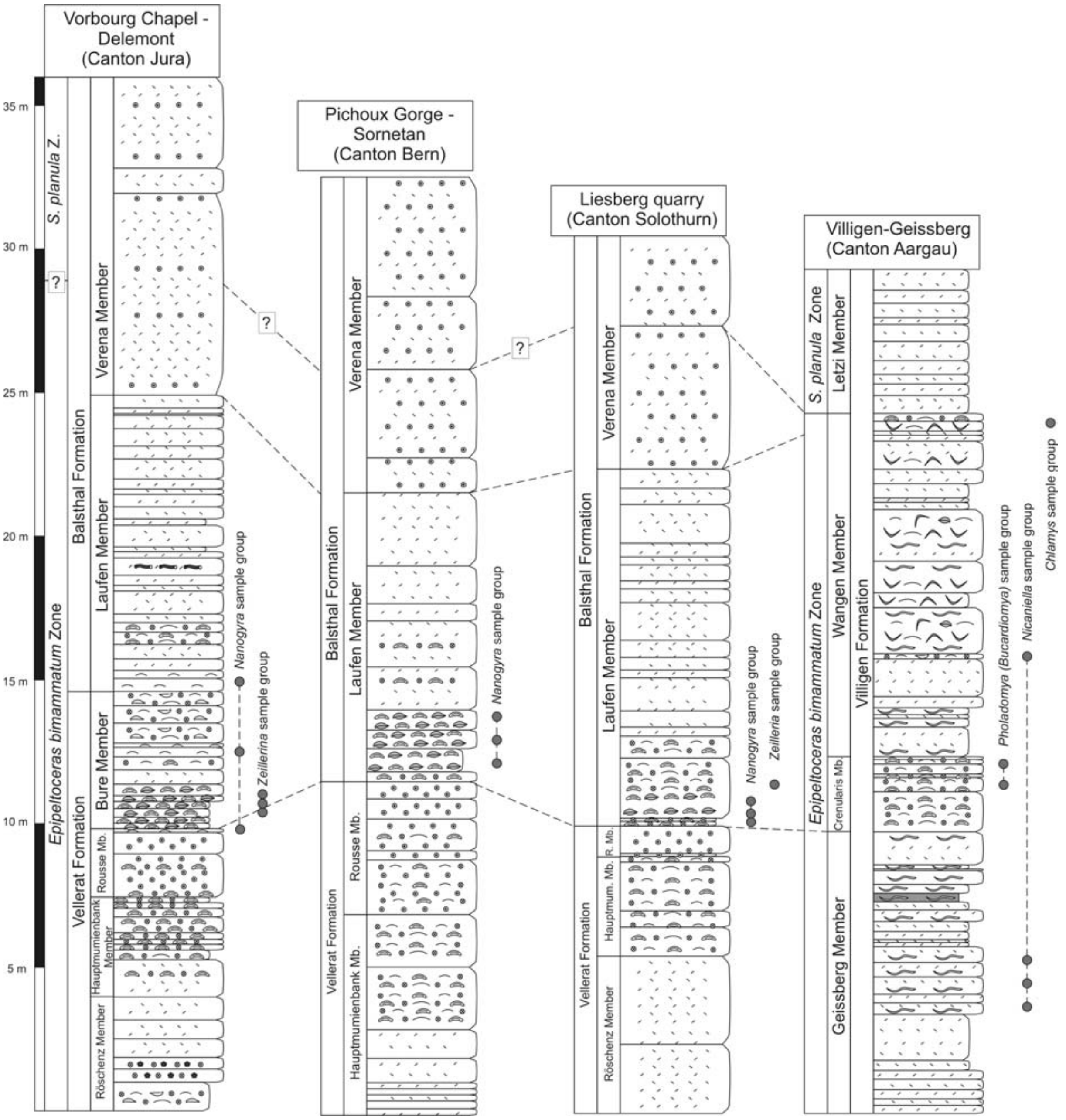


Figure 5 - Stratigraphic distribution of sample groups in four correlated sections with the Upper Oxfordian deposits. Three sections represent relatively shallow platform deposits of the Vellerat and Balsthal formations. One section represents deposits of the Villigen Formation that reflect deeper environments below storm wave base. Explanations: Fig. 3.

Upper Oxfordian (Vellerat, Balsthal and Villigen formations)

(6) Chapel Vorbourg. Small road outcrop near the Vorbourg Chapel expose an about 210 m-thick succession formed by the Middle Oxfordian-Lower Kimmeridgian deposits (Pittet et al., 1995; Pittet and Strasser, 1998a; Gygi, 2000a). The Upper Oxfordian Vellerat Formation is present in the upper part of the succession. The upper part of the Vellerat Formation (*E. bimammatum* Zone) consists of 5 m-thick oncoidal limestones of the Hauptmumienbank Member, and 3 m-thick oolite-oncoidal packstones of the Oolithe Rousse Member (Fig. 5). The top of this member is marked by one cm-thick concentration of in situ oysters (*Liostrea* sp.) that are markedly bored by lithophagiid bivalves. The Bure Member is formed in its lower part by marly coquinal floatstones with loosely packed and moderately sorted oncoids, and abundant brachiopods (*Zeillerina astartina, Septaliphoria arduennensis*) and bivalves (*Nanogyra nana, Radulopecten strictus*). Floatstones are bioturbated although small-scale stratification consisting of floatstones, wackestones and thick packstones is locally preserved. The abundance of oncoids decreases and the proportion of micrite increases in the upper part of the Bure Member. The Bure Member is overlain by an about 10 m-thick Laufen Member that consists of biomicritic limestones with dispersed brachiopods, bivalves, serpulids and oncoids. The Verena Member is formed by massive to thick-bedded dedolomitized limestones with ooids (Gygi, 2000a). The basal boundary of the *Subnebrodites planula* Zone is probably present in the lower parts of the Verena Member (Gygi, 2000a).

(7) Pichoux Gorge. Outcrops in the Pichoux Gorge NW of Sornetan in the Bern Canton expose an about 280-m thick, Middle Oxfordian-Lower Kimmeridgian succession (Pittet and Strasser, 1998a; Gygi, 2000a; Dupraz and Strasser, 2002). The upper part of the *Epipeltoceras bimammatum* Zone is formed by 7 m-thick oncoidal limestones of the Hauptmumienbank Member, 5 m-thick oomicritic limestones of the Oolithe Rousse Member, and about 10 m-thick, well-bedded bioclastic limestones of the Laufen Member (Fig. 5). The base of the Laufen Member is formed by 2.2 m-thick coquinal-oncoidal, loosely packed and poorly sorted, bioturbated floatstones that sharply overlie oolitic packstones. They contain abundant bivalves (*Nanogyra nana, Liostrea* sp*., Radulopecten strictus*), brachiopods (*Zeillerina astartina*), and serpulids. Brachiopods and bivalves are randomly oriented and affected by medium proportions of fragmentation and disarticulation. Small-scale alternation of poorly sorted floatstones with thin, well sorted layers is locally visible in limestone beds. The Laufen Member is overlain by thick-bedded oolitic-bioclastic limestones of the Verena Member. The base of the Kimmeridgian (*Subnebrodites planula* Zone) is probably lying near the base of the Verena Member (Gygi, 2000a).

(8) Liesberg quarry. A road outcrop near an entrance into the quarry in Liesberg is exposing the Upper Oxfordian Vellerat Formation and the Lower Kimmeridgian Balsthal Formation. The Hauptmumienbank Member is about 4 meters thick and is formed by biooomicritic floatstones and packstones with large oncoids several mm in size. The Oolithe Rousse Member consisting of well sorted and densely packed oolitic packstones is approximately 1 meter thick. The base of the Laufen Member is formed by oncoidal floatstones and packstones with thick oncoidal crusts, strongly bored bioclasts, and complex internal stratification (Fig. 5). The lower, 3-m thick part of the Laufen Member contains abundant brachiopods, bivalves, gastropods and serpulids. The upper part is formed by biomicritic, dedolomitized limestone beds (Gygi, 2000a). The Verena Member is formed by thick-bedded oolitic limestones.

(9) Villigen-Geissberg. Natural outcrops on the southern slopes of the Geissberg hill, about 800 m W of the Villigen village, N of Brugg in the Aargau Canton expose the Upper Oxfordian-Lower Kimmeridgian, carbonate-rich Villigen Formation (Gygi, 1969). The Villigen Formation starts with an about 10 m-thick Geissberg Member. It consists of light grey, thick-bedded, bioturbated mudstones and wackestones that locally contain abundant shallow burrowing bivalves (Fig. 5). It is overlain by 2.5 m-thick biomicritic floatstones of the Crenularis Member with abundant large-sized bivalves such as *Pholadomya (Bucardiomya) protei, Modiolus biparitus, Goniomya literata* and *Protocardia (P.) intexta*, rare brachiopods and dispersed sponges. Bioclasts are commonly coated by Fe-rich oncoidal crusts in this member. Based on ammonite findings, the Crenularis Member corresponds to the *E. bimammatum* Subzone (Gygi, 2000b). The Crenularis Member passes into 12 m-thick, light brown, well-bedded bioturbated mudstones and wackestones of the Wangen Member, locally with sponge fragments and abundant shallow burrowing bivalves. In the uppermost part of the Wangen Member, an about 50 cm-thick interval rich in coated bivalves, brachiopods, sponge fragments and limonitic nodules belongs to the so-called Knollen Bed. It represents a bed that marks the uppermost part of the *E. bimammatum* Zone (Gygi et al., 1998). In some sections of the eastern Swiss Jura, this bed can locally pass into small-scale sponge bioherms (Gygi, 1969, 2000b). The upper part of the Villigen Formation belongs to the *S. planula* Zone. It is formed by the Letzi Member that consists of well-bedded, shell-poor mudstones.

Methods

The absolute abundance of brachiopod and bivalve individuals was estimated with the maximum number of individuals (XNI) approach (i.e., each valve and shell was counted as one individual). 50 samples with a minimum sample-level number of 25 specimens were used in multivariate analyses. Brachiopods were determined by A.T. and bivalves by F.T.F. to species level. Deposits with benthic assemblages were assigned to different environments with respect to (1) siliciclastic supply (i.e., silty marls, marly limestones with silty admixture, and limestones), (2) wave-base level (i.e., habitats above normal storm wave base represented by amalgamated facies, habitats above maximum storm wave base represented by small-scale alternation of episodic and background facies, and habitats below maximum storm wave base represented by facies with no signs of storm disturbance), and (3) substrate consistency. Soft substrates are represented by mudstones and wackestobes, mixed substrates by oncoidal and bioclastic-rich floatstones and packstones, and hard substrates by coral boundstones.

Discrimination of sample groups

Nine sample groups sharing similar species abundances were discriminated with the Q-mode cluster analysis at Bray-Curtis similarity of about 35-50 (Fig. 6). The analysis was based on 50 samples with 2570 brachiopod and bivalve individuals. Five sample groups are dominated by pedunculate brachiopods, two sample groups by epifaunal bivalves, and two sample groups by infaunal bivalves (Figs. 7-8). Two samples collected in silty marls of the Sornetan Member (Middle Oxfordian) dominated by the free-lying bivalve *Entolium (Entolium) corneolum*, and the shallow burrowing eulamellibranch *Protocardia (Protocardia)* sp. are unique in composition. The sample dominated by *Entolium* is monospecific. In contrast, the sample dominated by *Protocardia* is highly diverse and contains 13 bivalve species.

(1) The *Argovithyris* sample group is represented by six samples with 542 individuals. Its sample-level richness ranges between 4 and 16, the evenness (PIE) is variable (0.34-0.75). The terebratulid *Argovithyris birmensdorfensis* dominates (58.4%). Other terebratulids are represented by *Zittelina orbis* (14.3%), *Placothyris rollieri* (5.8%), *Trigonellina loricata* (2.6%), and *Nucleata nucleata* (1.7%). Rhynchonellids are represented mainly by *Lacunosella arolica* (9.5%). Compositionally, this sample group dominated by terebratulids and *Lacunosella* is representative of sponge-dominated benthic assemblages that inhabited the northern Tethys shelf. Bivalves are represented mainly by epibyssate filibranchs (e.g., *Grammatodon (Cosmetodon)*, *Peudolimea*, 2.7%) and shallow burrowing protobranchs (e.g., *Isoarca*, 2.2%). Other bivalve guilds are rare (< 1%). This group occurs in bioturbated, sponge-rich marls and marly boundstones with variable amounts of microbial crusts. They correspond to habitats below MSWB. The group is limited to the Birmenstorf Member of the Wildegg Formation (*Gregoryceras transversanium* Zone, Middle Oxfordian).

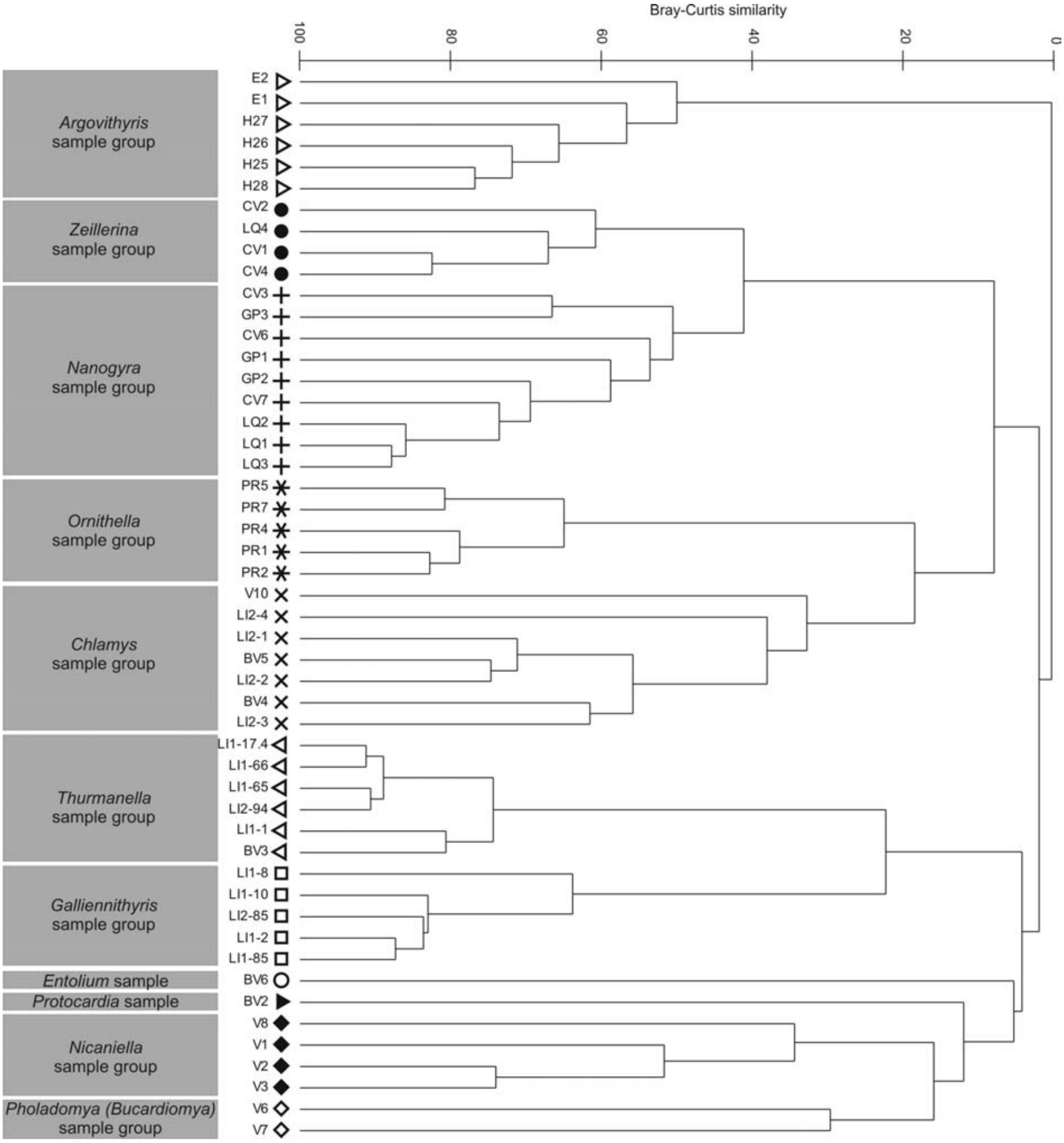


Figure 6 - Nine sample groups and two samples unique in composition discriminated by cluster analysis.

(2) The *Thurmanella* sample group is defined on the basis of six samples with 198 individuals. The sample-level richness is between one and five species, the evenness (PIE) is relatively low (0-0.46). This group is heavily dominated by the rhynchonellid *Thurmanella obtrita* (86%), followed by the less common epibyssate filibranchs *Oxytoma* sp. (1.9%), *Pseudolimea* sp. B (1.3%), *Radulopecten fibrosus* (1.2%), and *Grammatodon (G.)* sp. (1.2%), the free-lying bivalve *Entolium (E.) corneolum* (3%), and the shallow burrowing protobranch *Dacryomya* sp. (1.5%). Shallow burrowing eulamellibranchs and cementing filibranchs are rare (1%). This group occurs in shell-poor silty marls and silty marly limestones that reflect low-energy habitats below MSWB. It is limited to the Sornetan Member of the Bärschwill Formation and corresponds to the upper part of the Lower Oxfordian (top of the *C. cordatum* Zone) and the lower part of the Middle Oxfordian (bottom of the *G. transversarium* Zone).

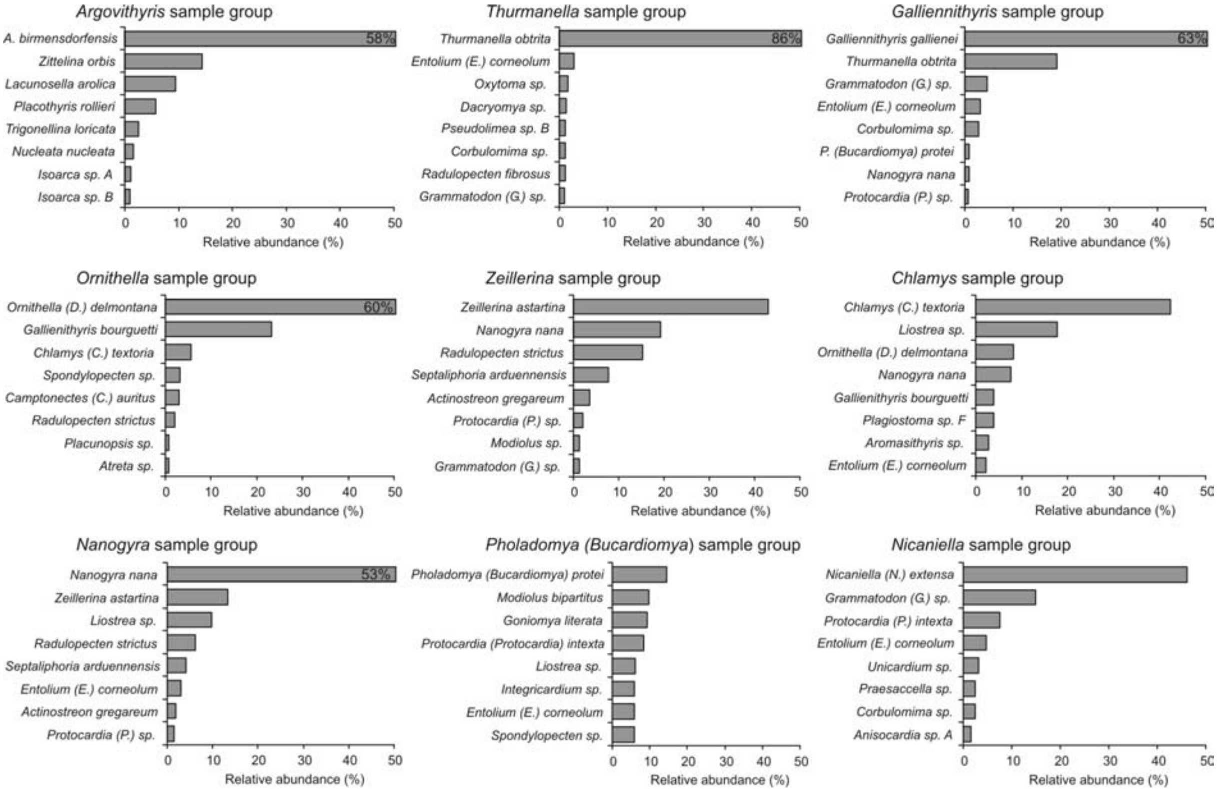


Figure 7 - Relative abundances of the eight most common species in nine sample groups.

(3) The *Galliennithyris* sample group consists of five samples with 189 individuals that occur in shell-poor silty marlstones/marly limestones of the Sornetan Member (Bärschwill Formation). The sample-level richness ranges between 5 and 7, the evenness (PIE) is moderately high (0.46-0.77). This group is dominated by the brachiopods *Galliennithyris gallienei* (63.4%) and *Thurmanella obtrita* (19.1%). Epibyssate filibranchs (6.3%) are mainly represented by *Grammatodon (G.)* sp., shallow burrowing eulamellibranchs (3.6%) by *Corbulomima* sp., and free-lying filibranchs (3.1%) by *Entolium (E.) corneolum*. Shallow burrowing protobranchs (1.4%) and deep burrowing eulamellibranchs (1.3%) are rare. Other bivalve guilds are scarce (> 1%). Similarly as the *Thurmanella* sample group, this group was limited to habitats below MSWB. It is also restricted to the

upper part of the Lower Oxfordian (top of the *C. cordatum* Zone) and the lower part of the Middle Oxfordian (bottom of the *G. transversarium* Zone).

(4) The *Ornithella* sample group is represented by five samples with 165 individuals. Its sample-level richness is between 4 and 7, the evenness (PIE) is moderate (0.41-0.7). It is dominated by the terebratulids *Ornithella (Delmontanella) delmontana* (59.6%) and *Galliennithyris bourguetti* (23.3%). The epibyssate bivalves *Chlamys (C.) textoria* (5.6%), *Spondylopecten* sp. (3.2%), *Camptonectes (C.) auritus* (2.9%), and *Radulopecten strictus* (2.1%) can be common. Cementing filibranchs are represented by *Placunopsis* sp. (0.7%) and *Atreta* sp. (0.7%). Other bivalve guilds are rare (< 1%). This group is limited to marly framestones with corals and serpulids, marly floatstones with coral debris, and well sorted bioclastic-intraclastic packstones of the Liesberg Member (Bärschwill Formation). This member belongs to the *P. antecedens* Subzone of the *G. transversarium* Zone (Middle Oxfordian).

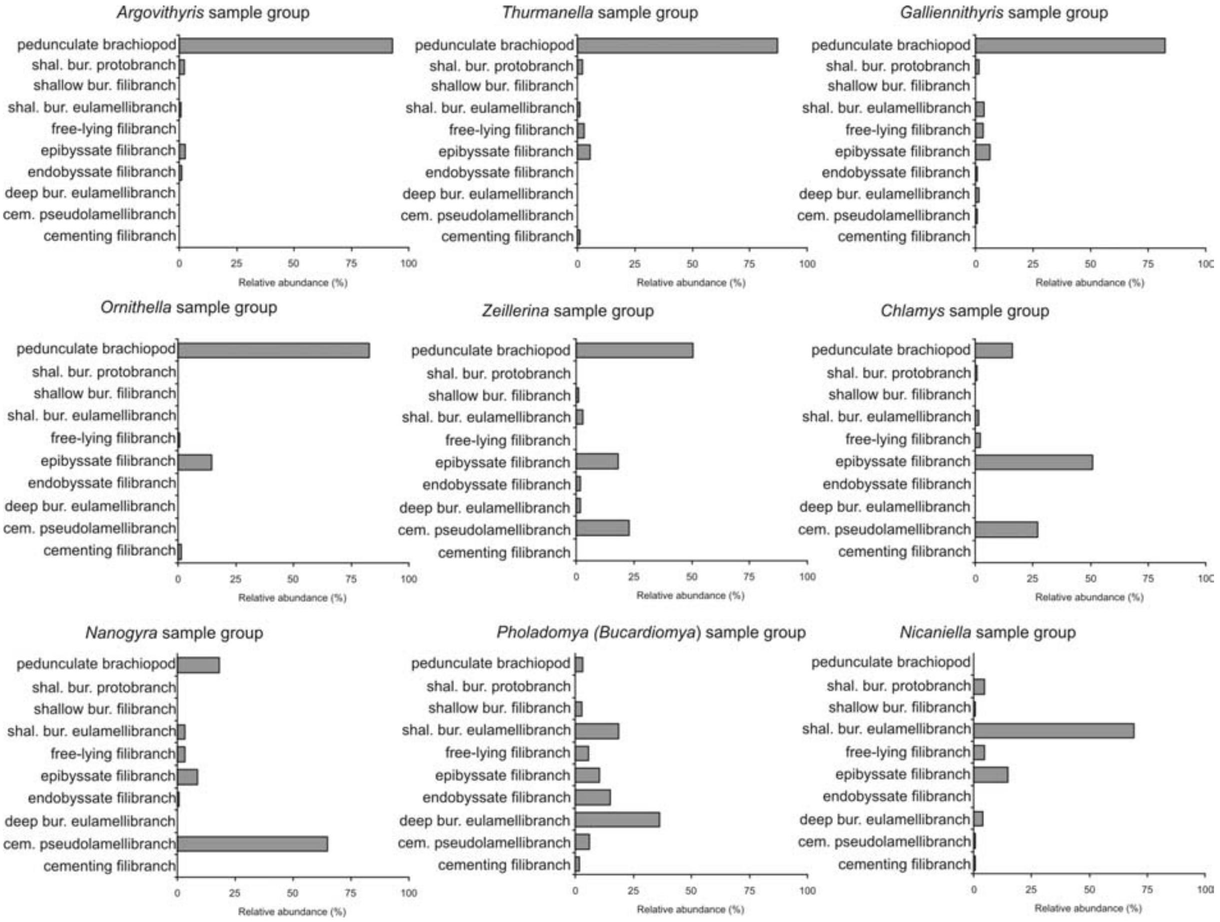

Argovithyris sample group
Thurmanella sample group
Galliennithyris sample group
Ornithella sample group
Zeillerina sample group
Chlamys sample group
Nanogyra sample group
Pholadomya (Bucardiomya) sample group
Nicaniella sample group

Figure 8 - Relative abundances of brachiopod and bivalve guilds in nine sample groups.

(5) The *Zeillerina* sample group is defined on the basis of four samples with 388 individuals. The sample-level richness is between 5 and 14, the evenness (PIE) is moderate to high (0.6-0.85). It is dominated by the terebratulid *Zeillerina astartina* (43.1%), the cementing pseudolamellibranch *Nanogyra nana* (19.2%), and the epibyssate filibranch *Radulopecten strictus* (15.3%). The rhynchonellid *Septaliphoria arduennensis* (7.7%), the cementing pseudolamellibranch *Actinostreon gregareum* (3.7%), and the shallow burrowing eulamellibranch *Protocardia (Protocardia)* sp. (2.1%) are less common. Shallow burrowing protobranchs and filibranchs, endobyssate filibranchs, and deep burrowing eulamellibranchs are rare (< 2%). This group occurs in oncoidal-bioclastic floatstones of

the stratigraphically comparable Bure (Vellerat Formation) and Laufen members (Villigen Formation). They correspond to habitats above MSWB and NSWB and belong to the middle parts of the *E. bimammatum* Zone (Upper Oxfordian).

(6) The *Nanogyra* sample group is represented by nine samples with 539 individuals. Its sample-level richness attains 4 to 13 species, the evenness (PIE) is moderate to high (0.42-0.81). This group is dominated by the cementing pseudolamellibranchs *Nanogyra nana* (53.3%) and *Liostrea* sp. (9.7%), the pedunculate brachiopods *Zeillerina astartina* (13.3%) and *Septaliphoria arduennensis* (4.1%), and the epibyssate bivalve *Radulopecten strictus* (6.1%). Free-lying bivalves are mainly represented by *Entolium (E.) corneolum* (3.1%), and shallow burrowing eulamellibranchs by *Protocardia (P.)* sp. (1.6%). Other bivalve guilds are rare (< 1%). This group occurs in oncoidal-bioclastic floatstones and packstones of the Bure (Vellerat Formation) and Laufen members (Villigen Formation). These deposits correspond to shallow habitats above NSWB and MSWB and belong to the *Epipeltoceras bimammatum* Zone.

(7) The *Chlamys* sample group consists of seven samples with 219 individuals. The sample-level richness ranges between 4 and 13, the evenness (PIE) is moderate to high (0.47-0.85). The epibyssate filibranch *Chlamys (C.) textoria* (42.4%) and the cementing pseudolamellibranch *Liostrea* sp. (17.8%) are abundant. The terebratulids *Ornithella (Delmontanella) delmontana* (8.2%) and *Galliennithyris bourguetti* (4%), the cementing pseudolamellibranch *Nanogyra nana* (7.7%), and the epibyssate filibranch *Plagiostoma* sp. F are less common. Free-lying filibranchs are represented by *Entolium (E.) corneolum* (2.2%). Other bivalve guilds are rare (< 2%). This group mainly occurs in marly, coral-serpulid framestones and floatstones of the Liesberg Member. Framestones and floatstones were assigned to habitats above MSWB. One sample is derived from bioclastic-sponge floatstone of the Wangen Member (Villigen Formation, Upper Oxfordian, *E. bimammatum* Zone).

(8) The *Nicaniella* sample group is represented by four samples with 159 individuals. Its sample-level richness ranges between 8 and 10 species, the evenness (PIE) is moderate to high (0.4-0.89). This group is dominated by shallow burrowing eulamellibranchs (69.2%). They are represented mainly by *Nicaniella (N.) extensa* (46.1%), *Protocardia (P.) intexta* (7.6%), *Unicardium* sp. (3.1%), *Praesaccella* sp. (2.5%), and *Corbulomima* sp. (2.4%). Epibyssate filibranchs are represented by *Grammatodon (G.)* sp. (14.9%) and free-lying filibranchs by *Entolium (E.) corneolum* (4.7%). Shallow burrowing protobranchs (4.8%) and deep burrowing eulamellibranchs (4.1%) can also be common. Brachiopods are absent. This group occurs in shell-poor mudstones/wackestones of the Geissberg and Wangen members of the Villigen Formation (Upper Oxfordian, *E. bimammatum* Zone). These deposits correspond to carbonate-rich habitats below MSWB.

(9) The *Pholadomya (Bucardiomya)* sample group is defined on the basis of two samples and 87 individuals collected in oncoidal-bioclastic floatstones of the Crenularis Member (Villigen Formation, Upper Oxfordian, *E. bimammatum* Zone). These deposits correspond to habitats below MSWB. The sample-level richness ranges between 12 and 15 species, the evenness (PIE) is very high (0.87-0.96). Deep burrowing eulamellibranchs (36.2%) represented by *Pholadomya (Bucardiomya) protei* (14.5%), *Goniomya literata* (9.3%), *Pleuromya uniformis* (4.7%), *Pholadomya (P.)* sp. (3.9%) and *Cercomya undulata* (3.9%) are most abundant. Shallow burrowing eulamellibranchs (18.6%) are represented mainly by *Protocardia (P.) intexta* (8.5%) and *Integricardium* sp. (5.8%), and endobyssate filibranchs by *Modiolus bipartitus* (9.8%) and *Gervillella* sp. (5.2%). Other bivalve guilds such as epibyssate filibranchs (*Spondylopecten* sp., *Grammatodon (G.)* sp.), free-lying filibranchs (*Entolium (E.) corneolum*), and cementing pseudolamellibranchs (*Liostrea* sp.) are also common. Pedunculate brachiopods are represented by the terebratulid *Aromasithyris* sp. (3.3%).

Ordination of the Oxfordian samples

The Oxfordian samples of the Swiss Jura strongly group according to their lithostratigraphic membership in Q-mode NMDS of all samples based on species abundances. Samples belonging to the Middle Oxfordian Birmenstorf, Sornetan, and Liesberg members, and to the Upper Oxfordian Villigen Formation and Laufen and Bure members are markedly segregated (Fig. 9A). The *Argovithyris* sample group is restricted to the Birmenstorf Member, the *Thurmanella* and *Galliennithyris* sample groups to the Sornetan Member, the *Ornithella* sample groups to the Liesberg Member, the *Zeillerina* sample group to the Bure and Laufen members, and the *Pholadomya (Bucardiomya)* and *Nicaniella* sample groups to the Villigen Formation. Brachiopod and bivalve sample groups are not consistently segregated in Q-mode NMDS. In Q-mode NMDS of all samples based on guild abundances, samples dominated by pedunculate brachiopods continuously grade into samples dominated by the epibyssate bivalve *Chlamys (C.) textoria* in the Liesberg Member and the cementing bivalve *Nanogyra nana* in the Bure and Laufen members (Fig. 9B). These samples are rather dissimilar in guild composition to samples from the Villigen Formation that are dominated by the shallow burrowing bivalve *Nicaniella (N.) extensa* and the deep burowing bivalve *Pholadomya (Bucardiomya) protei*. Owing to this stratigraphic segregation, multivariate analyses of brachiopod and bivalve abundance patterns were separately performed for the Lower – lower Middle Oxfordian Bärschwill Formation, and the Upper Oxfordian carbonate-rich formations.

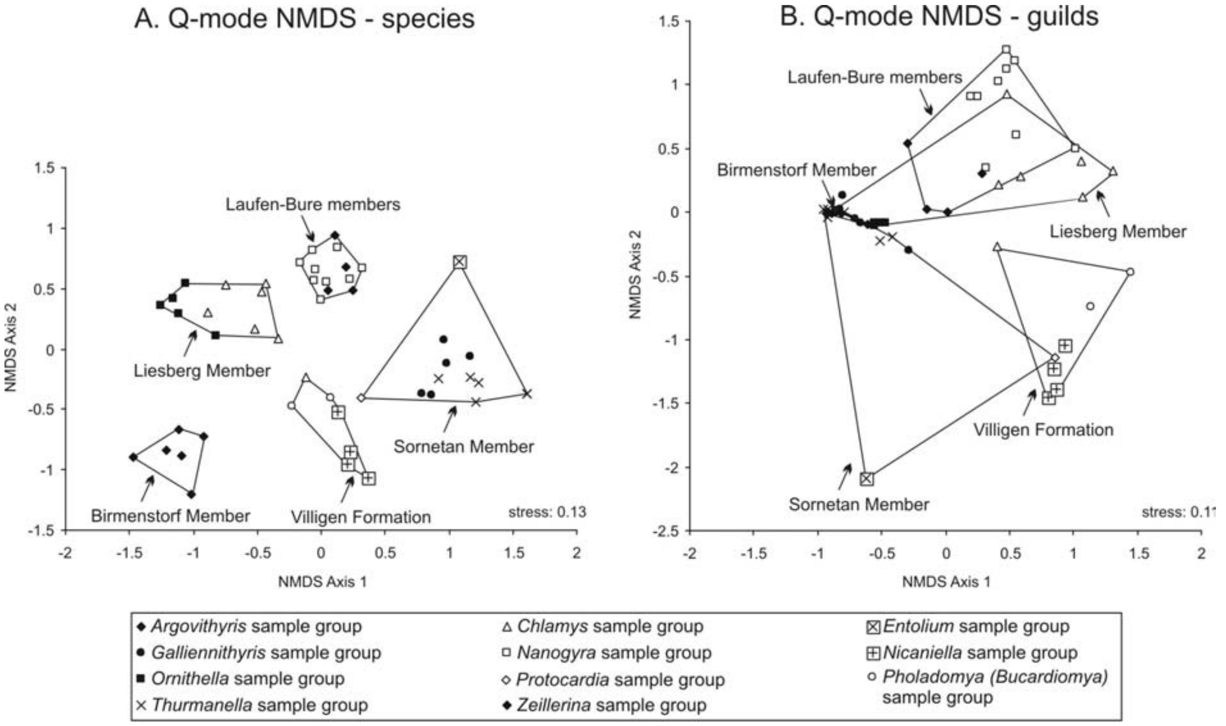


Figure 9 - Compositional relationship among all Oxfordian samples of the Swiss Jura based on species and guild abundances. A. Q-mode non-metric multidimensional scaling (NMDS) of 50 samples based on species abundances. B. Q-mode NMDS of 50 samples based on guild abundances.

Co-occurrence patterns of brachiopods and bivalves

Owing to substantial stratigraphic effects on composition of benthic communities, R-mode analyses based on abundances of species > 5% per sample was performed separately for (1) the Lower-lower Middle Oxfordian Bärschwill Formation (Fig. 10A-B), and (2) the Upper Oxfordian Villigen, Vellerat and Balsthal formations (Fig. 10C-D). For species of the Bärschwill Formation, there are no differences among abundance patterns of brachiopods, protobranchs, filibranchs, pseudolamellibranchs and eulamellibranchs (R = -0.041, p = 0.86, Tab. 1). In contrast, the differences among abundance patterns of five simplified guilds with distinct gill type are very low but significant for the Upper Oxfordian dataset (R = 0.16, p = 0.019, Tab. 1). This partial segregation in abundance pattens is also visible in R-mode NMDS based on species abundances (Fig. 10C). Pairwise between-guild comparisons indicate that this segregation is mainly between pedunculate brachiopods and eulamellibranchs (R = 0.33, p = 0.0093), and between pseudolamellibranchs and eulamellibranchs (R = 0.31, p = 0.034). R-mode NMDS based on guild abundances and Bray-Curtis similarities (BC) indicate that in the Bärschwill Formation, pedunculate brachiopods co-occurred commonly both with epifaunal and infaunal bivalves. In the Upper Oxfordian, brachiopods shared abundance patterns mainly with cementing pseudolamellibranchs (BC = 53) and epibyssate filibranchs (BC = 47). In contrast, brachiopods co-occurred rarely with shallow burrowing protobranchs (BC = 7), shallow burrowing eulamellibranch bivalves (BC = 12), and deep burrowing eulamellibranch bivalves (BC = 14). Samples of the Birmenstorf Member were not analyzed for guild co-occurrence patterns because only one bivalve species exceeds 5% per sample.

R-mode based one-way ANOSIM testing differences in species abundance among guilds	R	p-value	Number of permutations	Number of permuted R≥observed R
Villigen, Vellerat, Balsthal formations - Upper Oxfordian				
Global test	0.159	0.0192	10000	192
brachiopod vs. filibranch	-0.156	0.87	495	428
brachiopod vs. pseudolamellibranch	0.185	0.2	35	7
brachiopod vs. eulamellibranch	0.33	0.0093	3876	36
filibranch vs. pseudolamellibranch	-0.112	0.7	165	116
filibranch vs. eulamellibranch	0.049	0.27	10000	2660
pseudolamellibranch vs. eulamellibranch	0.308	0.034	816	28
Bärschwill Formation - Lower - lower Middle Oxfordian				
Global test	-0.041	0.65	10000	6475
brachiopod vs. filibranch	-0.112	0.86	1001	860

Table 1 - Analyses of similarities (ANOSIM) testing differences in abundance patterns among protobranchs, filibranchs, pseudolamellibranchs, eulamellibranchs and brachiopods. This test is performed separately for the Lower – lower Middle Oxfordian and the Upper Oxfordian dataset.

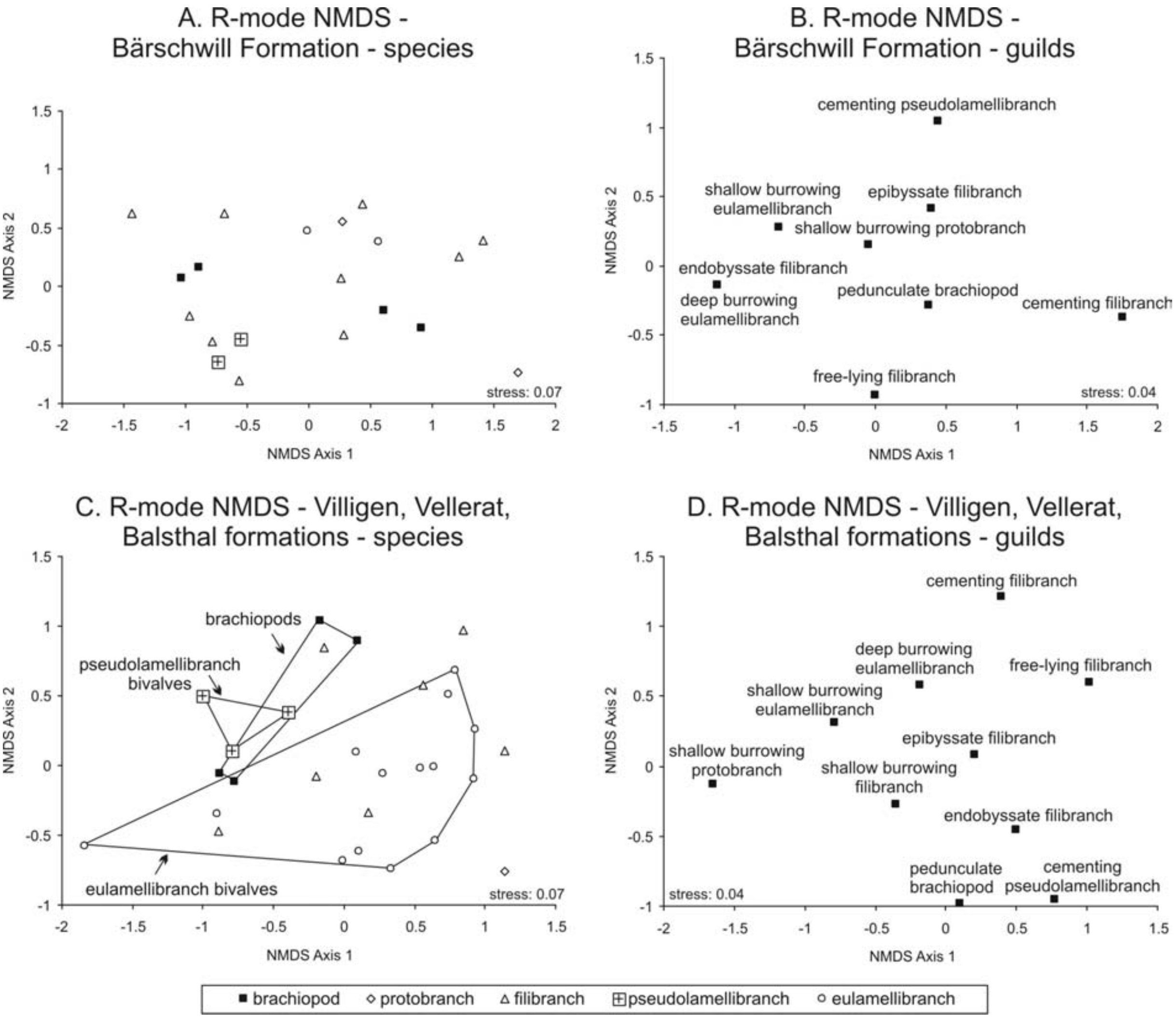


Figure 10 - Comparison of abundance patterns of brachiopod and bivalve species and guilds in R-mode non-metric multidimensional scaling (NMDS). The Lower – lower Middle Oxfordian dataset (Bärschwill Formation) and the Upper Oxfordian dataset (Villigen, Vellerat and Balsthal formations) are analyzed separately. Species are labeled according to their membership with respect to their gill type. A. R-mode NMDS of species of the Bärschwill Formation. B. R-mode NMDS of guilds of the Bärschwill Formation. C. R-mode NMDS of species of the Villigen, Vellerat and Balsthal formations. D. R-mode NMDS of guilds of the Villigen, Vellerat and Balsthal formations.

Environmental effects

Similarly as R-mode based analyses of co-occurrence patterns, environmental effects on species abundances were evaluated separately for (1) the Lower – lower Middle Oxfordian Bärschwill Formation, and (2) the Upper Oxfordian Villigen, Vellerat and Balsthal formations. Samples of the Birmenstorf Member dominated by the terebratulid *Argovithyris* are markedly segregated in species composition from other samples in Q-mode NMDS (Fig. 9A). These samples were further not analyzed because they correspond to relatively uniform environmental conditions with respect to substrate and wave-base level. Habitats of benthic assemblages of the Bärschwill Formation differ mainly in the degree of siliciclastic supply and wave-base level. In this case, wave-basel level variations correlate with substrate consistency because hard-bottom environments with corals correspond to habitats above MSWB (Liesberg Member), and soft-bottom, mud-rich environments correspond to habitats below MSWB (Sornetan Member). Therefore, effects of siliciclastic supply and wave-base level/substrate consistency on species abundances of the Bärschwill Formation were evaluated only. Benthic assemblages of the Upper Oxfordian deposits are predominantly derived from limestones and their habitats differ mainly in substrate consistency and wave-base level. In this case, effects of wave-base level and substrate consistency were assessed separately.

Bärschwill Formation

Effects of wave-base level and substrate consistency. One-way ANOSIM demonstrates that there are high and significant differences in species ($R = 0.92$, $p < 0.0001$, Tab. 2) and relatively low but also significant differences in guild abundances ($R = 0.21$, $p = 0.006$, Tab. 2) between hard-bottom, coral-rich habitats above MSWB (Liesberg Member) and soft-bottom habitats below MSWB (Sornetan Member). Between-habitat differences are also visualized in Q-mode NMDS plots (Fig. 11A-B). Habitats above MSWB were represented by two samples only and were not included into this analysis. Hard-bottom habitats above MSWB were dominated by epibyssate and cementing bivalves and the brachiopods *Ornithella (Delmontanella) delmontana* and *Galliennithyris bourgueti* (Figs. 12-13). Soft-bottom habitats below MSWB were dominated by the brachiopods *Thurmanella obtrita* and *Galliennithyris galliennei*, and shallow burrowing and free-lying bivalves.

Effects of siliciclastic supply. One-way ANOSIM indicates very high and significant effects of siliciclastic supply on species abundances ($R = 0.83$, $p < 0.0001$). The rhynchonellid brachiopod *Thurmanella obtrita* dominates in silty marls and marly limestones of the Sornetan Member. The terebratulid *Galliennithyris galliennei* increases in abundance with increasing carbonate content. Limestones of the Liesberg Member are characterized by abundance of species that are completely absent or rare in the Sornetan Member. They include the epifaunal bivalves *Chlamys (C.) textoria*, *Liostrea* sp. and *Nanogyra nana*, and the terebratulids *Ornithella (Delmontanella) delmontana* and *Galliennithyris bourgueti*. In addition, pairwise comparisons indicate that although the main compositional differences are lying between marls and marly limestones on one hand and limestones on the other, marls and marly limestones show also consistent differences in species and guild composition. Two-way ANOSIM allowing for variations in substrate/wave-base level shows low but significant effects of siliciclastic supply on species abundances ($R = 0.29$, $p = 0.028$). This two-way test is limited to soft-bottom habitats only and thus effectively tests differences between silty marls and marly limestones. Habitats varying in siliciclastic supply show also significant differences in guild abundances (R[one-way ANOSIM] = 0.25, $p = 0.0066$, R[two-way ANOSIM] = 0.3, $p = 0.026$, Tab. 2). Note that brachiopods are relatively abundant along the whole gradient with varying siliciclastic supply, but different species reach their abundance peak in limestones, marly limestones and marls (Fig. 12). Cementing and epibyssate bivalves are most abundant in limestones, shallow burrowing and free-lying bivalves in marls, and pedunculate brachiopods attain abundance peak in marly limestones with silty admixture (Figs. 12-13).

Vellerat, Balsthal and Villigen formations

Effects of wave-base level. Q-mode NMDS based on species and guild abundances (Fig. 11C-D) and one-way ANOSIM shows that there are relatively high differences in community composition between habitats differing in the wave-base level based on species ($R = 0.57$, $p < 0.0001$, Tab. 3) and guild abundances ($R = 0.52$, $p < 0.0001$, Tab. 3). The main difference in community composition is between shallow habitats above MSWB and above NSWB on one hand, and deep habitats below MSWB on the other. The pedunculate brachiopod *Zeillerina astartina* and the cementing bivalve

Nanogyra nana are most abundant in shallow habitats above NSWB and MSWB (Figs. 14-15). In contrast, shallow burrowing and deep burrowing eulamellibranchs increase in abundance towards deeper habitats below MSWB. Epibyssate bivalves do not substantially vary in abundance between habitats below and above MSWB. In addition, keeping variations in substrate consistency constant, differences between habitats differing in the wave base level are also moderately high and significant both for species and guild abundances (two-way ANOSIM, R [species] = 0.44, p = 0.0007, R[guilds] = 0.37, p = 0.004, Tab. 3).

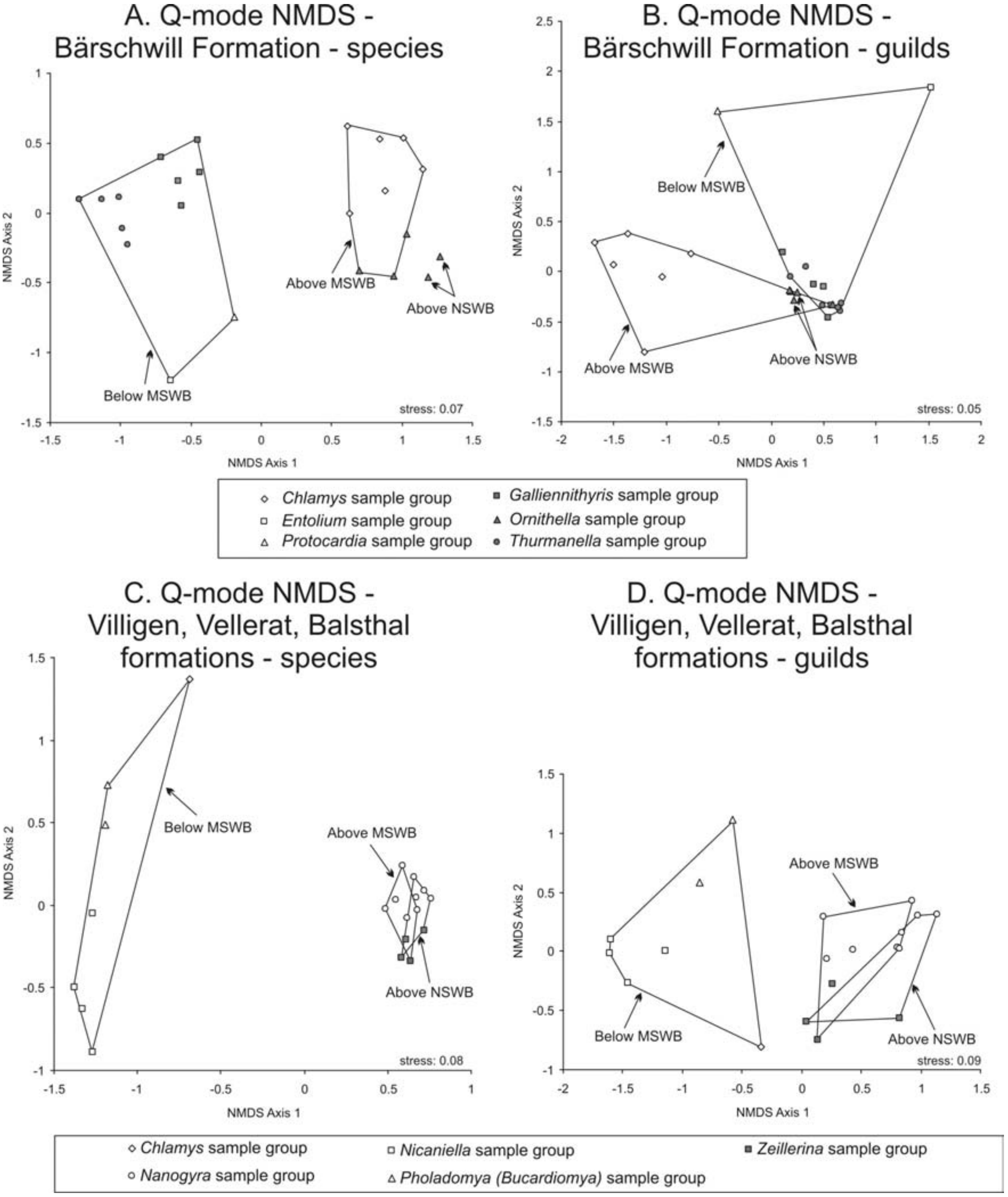


Figure 11 - Q-mode non-metric multidimensional scaling (NMDS) showing between-habitat differences in species and guild composition during the two Oxfordian time intervals. A. Q-mode NMDS of the Lower – lower Middle Oxfordian samples (Bärschwill Formation) based on species abundances. B. Q-mode NMDS of the Lower – lower Middle Oxfordian samples (Bärschwill Formation) based on guild abundances. C. Q-mode NMDS of the Upper Oxfordian samples (Villigen, Vellerat and Balsthal formations) based on species abundances. D. Q-mode NMDS of the Upper Oxfordian samples (Villigen, Vellerat and Balsthal formations) based on guild abundances.

One-way ANOSIM - effects of sediment supply	R	p-value	Number of permutations	Number of permuted R≥observed R
Species				
Global test	0.83	<0.0001	10000	0
silty marl vs. marly limestone	0.287	0.0279	1287	36
silty marl vs. limestone	0.966	0.00023	4368	1
marly limestone vs. limestone	0.993	0.0001	10000	1
Guilds				
Global test	0.245	0.0066	10000	66
silty marl vs. marly limestone	0.297	0.026	1287	34
silty marl vs. limestone	0.265	0.047	4368	207
marly limestone vs. limestone	0.267	0.016	10000	155

Two-way ANOSIM - effects of sediment supply, allowing for variations in substrate/wave-base level	R	p-value	Number of permutations	Number of permuted R≥observed R
Species - silty marl vs. marly limestone	0.287	0.028	1287	36
Guilds - silty marl vs. marly limestone	0.297	0.026	1287	34

One-way ANOSIM - effects of substrate/wave-base level	R	p-value	Number of permutations	Number of permuted R≥observed R
Species				
Hard-bottom (above MSWB) vs. soft-bottom (below MSWB)	0.918	<0.0001	10000	0
Guilds				
Hard-bottom (above MSWB) vs. soft-bottom (below MSWB)	0.208	0.0061	10000	61

Table 2 - Analyses of similarities (ANOSIM) testing effects of varying siliciclastic supply and wave-base level on species and guild composition in the Lower – lower Middle Oxfordian dataset. The effects of siliciclastic supply is assessed with one-way and two-way analyses, the effects of wave-base level is evaluated with one-way analyses only.

Effects of substrate consistency. One-way ANOSIM indicates that habitats differing in the substrate consistency significantly differ in species (R = 0.76, p = 0.0004, Tab. 3) and guild abundances (R = 0.79, p = 0.0002, Tab. 3). When the wave-base level is kept constant and the analysis is thus restricted to habitats below MSWB, the difference between soft-bottom and mixed bottom habitats is also relatively high for species (R = 0.75, p = 0.029) and guild abundances (R = 0.8, p = 0.029). Shallow burrowing eulamellibranchs substantially increase, and pedunculate brachiopods and cementing bivalves decrease in abundance with decreasing substrate consistency (Figs. 14-15). The abundance of epibyssate bivalves remains relatively constant with varying substrate consistency.

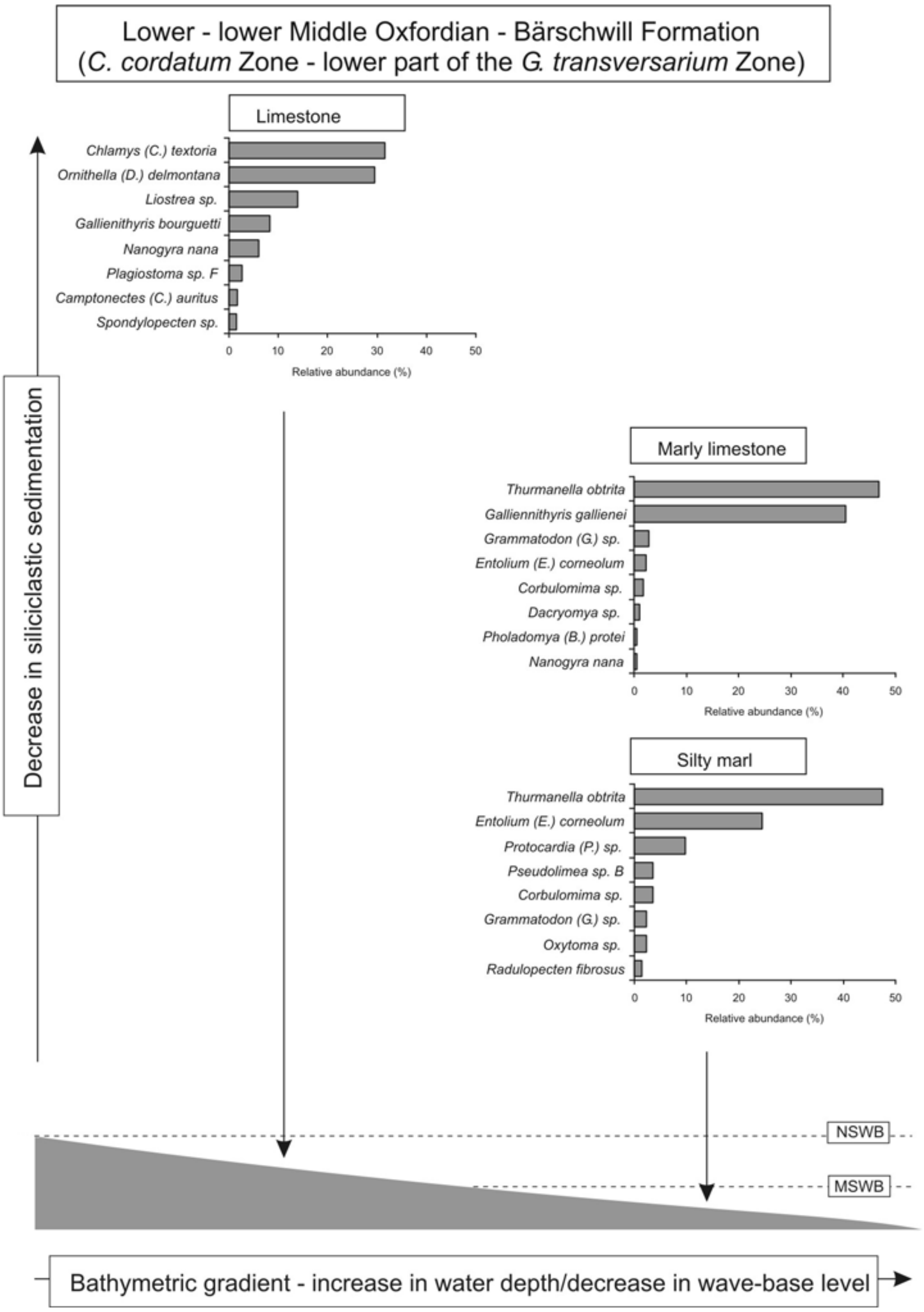


Figure 12 - Between-habitat differences in abundances of species with respect to varying wave-base level and siliciclastic supply during the Early – early Middle Oxfordian (Bärschwill Formation).

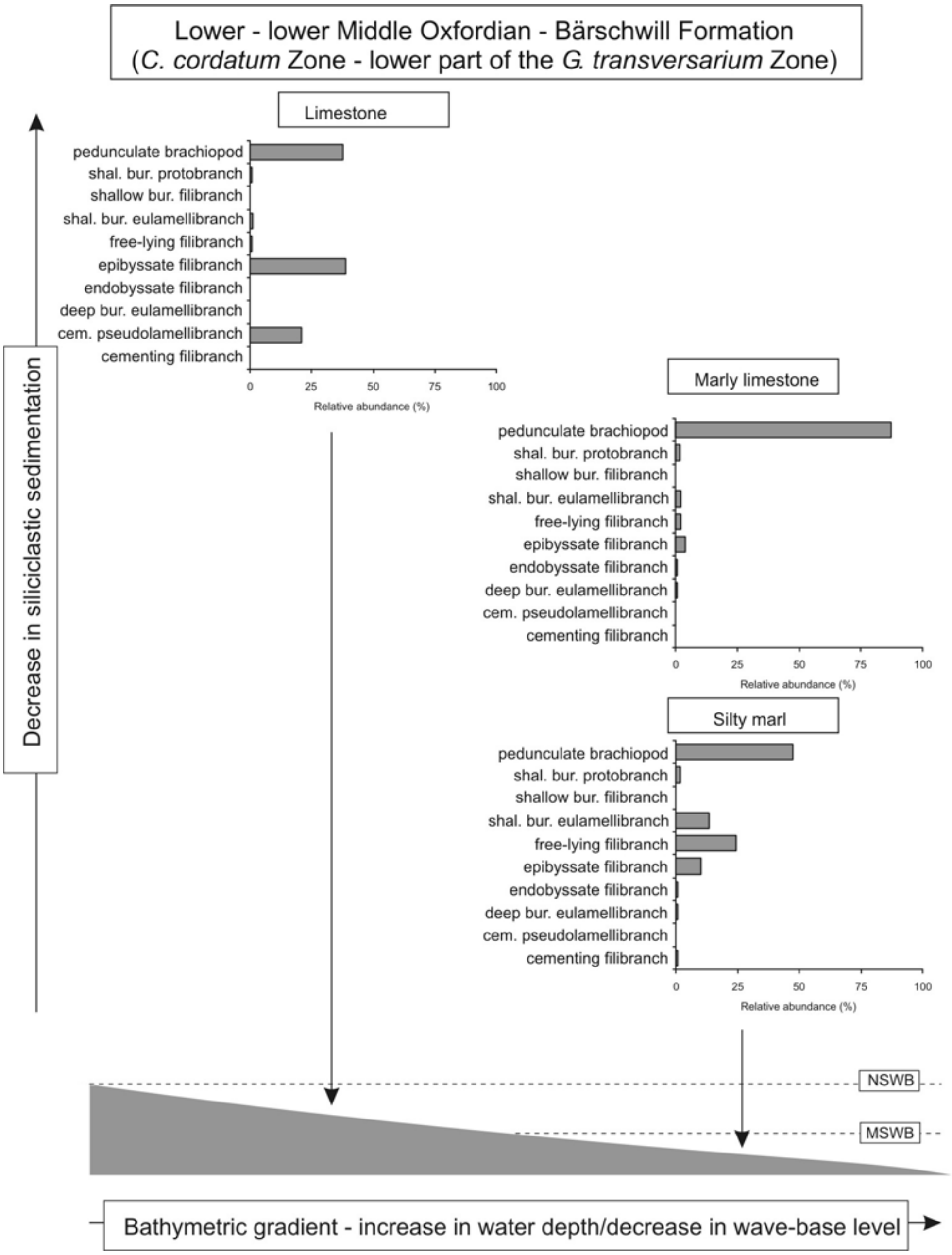


Figure 13 - Between-habitat differences in abundances of guilds with respect to varying wave-base level and siliciclastic supply during the Early – early Middle Oxfordian (Bärschwill Formation).

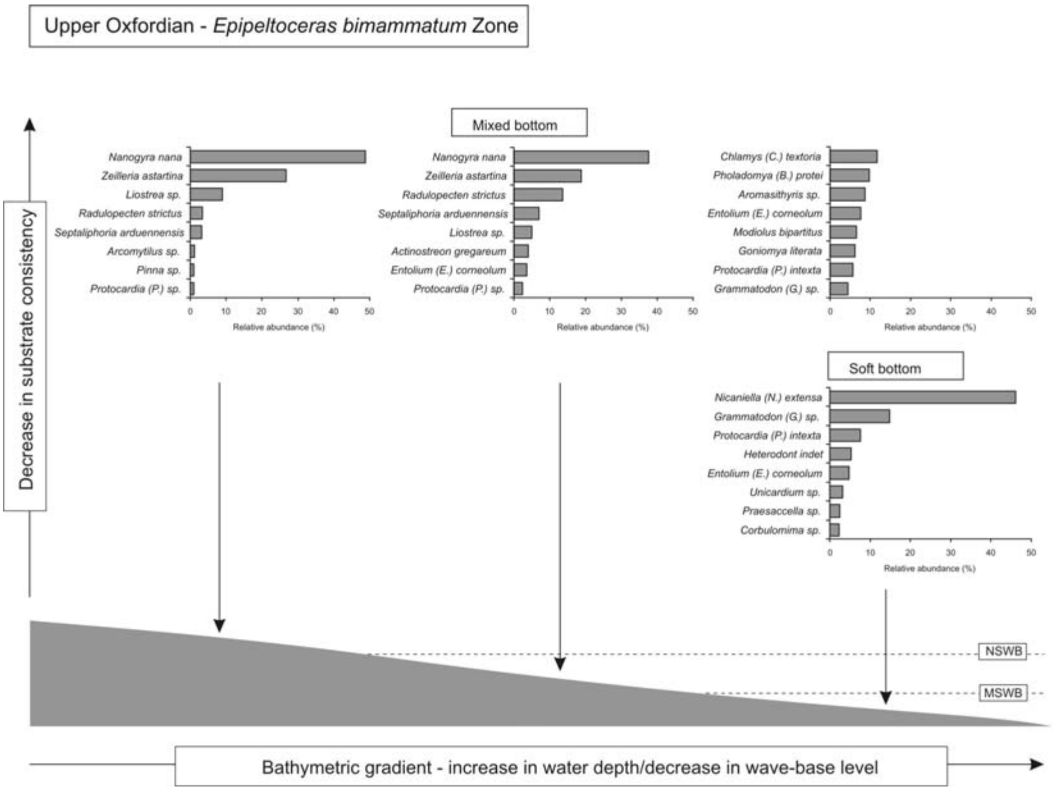


Figure 14 - Between-habitat differences in abundances of species with respect to varying wave-base level and substrate consistency during the Late Oxfordian (Villigen, Vellerat and Balsthal formations).

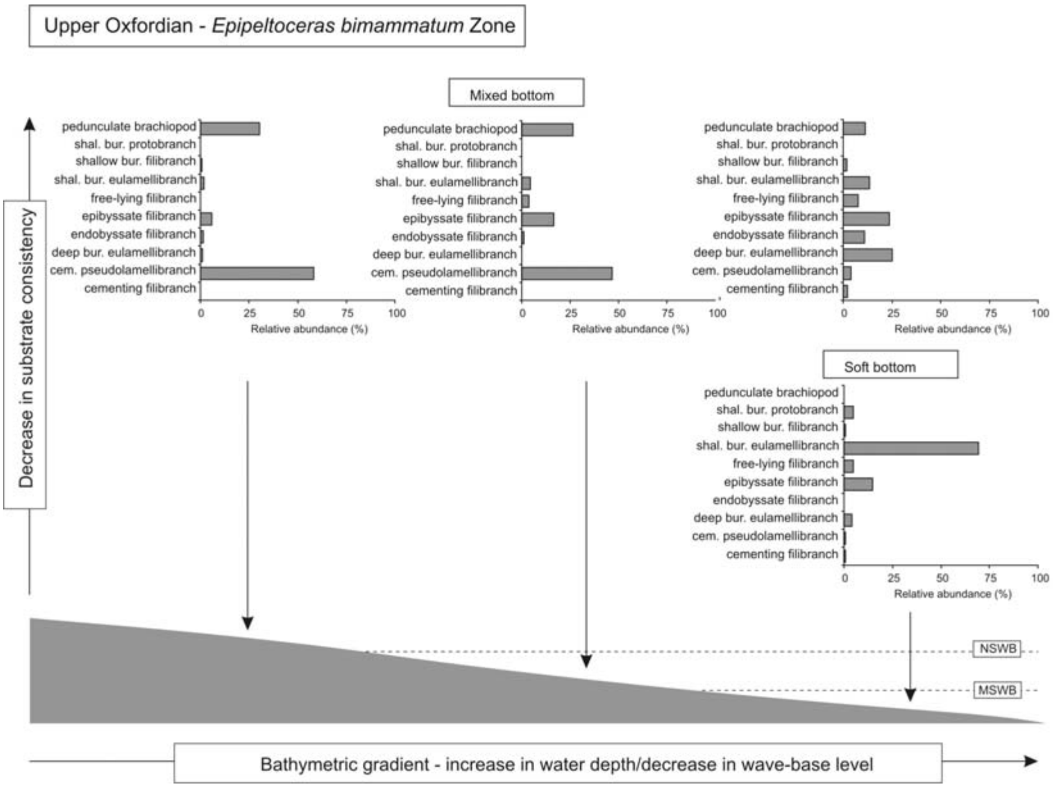


Figure 15 - Between-habitat differences in abundances of guilds with respect to varying wave-base level and substrate consistency during the Late Oxfordian (Villigen, Vellerat and Balsthal formations).

One-way ANOSIM - effects of wave-base level	R	p-value	Number of permutations	Number of permuted R≥observed R
Species				
Global test	0.569	<0.0001	10000	0
Above MSWB, Above NSWB	-0.009	0.46	1716	784
Above MSWB, Below MSWB	0.931	0.0006	1716	1
Above NSWB, Below MSWB	0.961	0.0006	1716	1
Guilds				
Global test	0.519	<0.0001	10000	0
Above MSWB, Above NSWB	-0.011	0.42	1716	717
Above MSWB, Below MSWB	0.741	0.0006	1716	1
Above NSWB, Below MSWB	0.858	0.0011	1716	2

Two-way ANOSIM - effects of wave-base level, allowing for variations in substrate	R	p-value	Number of permutations	Number of permuted R≥observed R
Species				
Global test	0.435	0.0007	10000	7
Above MSWB, Above NSWB	-0.009	0.46	1716	784
Above MSWB, Below MSWB	0.976	0.0083	120	1
Above NSWB, Below MSWB	0.997	0.012	84	1
Guilds				
Global test	0.374	0.004	10000	39
Above MSWB, Above NSWB	-0.011	0.42	1716	717
Above MSWB, Below MSWB	0.802	0.0083	120	1
Above NSWB, Below MSWB	0.84	0.012	84	1

One-way ANOSIM - effects of substrate	R	p-value	Number of permutations	Number of permuted R≥observed R
Species				
Mixed-bottom vs. soft-bottom	0.761	0.0004	4845	2
Guilds				
Mixed-bottom vs. soft-bottom	0.79	0.0002	4845	1

Two-way ANOSIM - effects of substrate, allowing for variations in wave-base level	R	p-value	Number of permutations	Number of permuted R≥observed R
Species				
Mixed-bottom vs. soft-bottom	0.75	0.029	35	1
Guilds				
Mixed-bottom vs. soft-bottom	0.796	0.029	35	1

Table 3 - Analyses of similarities (ANOSIM) testing effects of varying substrate consistency and wave-base level on species and guild composition in the Upper Oxfordian dataset. These effects are assessed with one-way and two-way analyses.

Discussion

Bärschwill Formation. During the Early and early Middle Oxfordian, glauconitic-rich sedimentation took place in the eastern part of the Swiss Jura. However, quantitative data about community composition are not available owing to marked stratigraphic condensation and low abundance of macrobenthic fauna. In contrast, deposits in the western part of the Swiss Jura are thick and contain abundant brachiopods and bivalves. The deposition of marls and marly mudstones of the

Sornetan Member in the western part of the Swiss Jura was temporally replaced by coral framestones and floatstones of the Liesberg Member (Gygi, 1990a). In this area, variations in community coposition generally reflect this change in sedimentation regime. On one hand, the decrease in abundances of brachiopods and the increase in abundances of infaunal and epifaunal bivalves with increasing siliciclastic supply from marly limestones to marls is in accord with a lower tolerance of brachiopods to high particle concentrations when compared to bivalves (Rhodes and Thompson, 1992, 1993). On the other hand, the decrease in abundances of brachiopods and the increase in abundance of epifaunal bivalves towards shallow, coral-rich habitats with hard substrate might be related to combined effects of higher flow velocity that might be preferred by bivalves, and higher grazing and competition intensity for space in hard-bottom habitats that is more deleterious for brachiopods than for epifaunal bivalves. Rarity of infaunal bivalves in coral habitats can be related to a reduced availability of soft substrate.

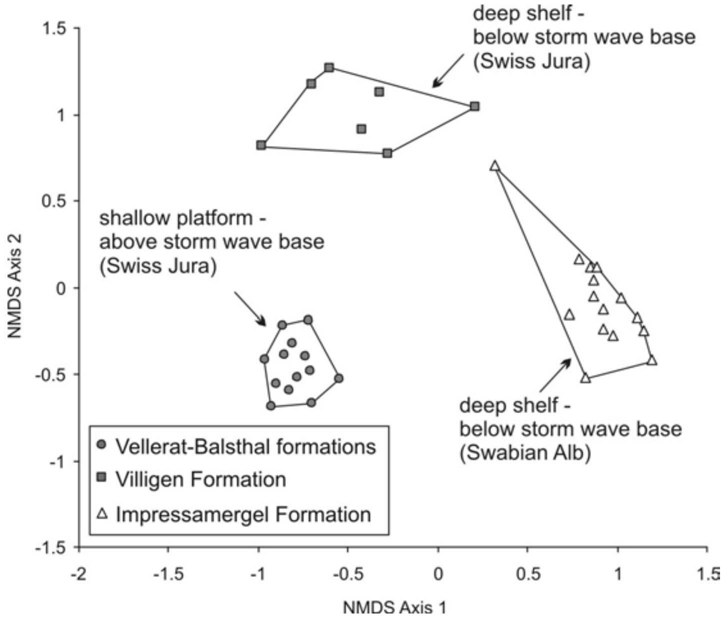


Figure 16 - Differences in species composition between the Swiss Jura and the Swabian Alb in the *Epipeltoceras bimammatum* Zone. Note that deep-shelf assemblages of the Villigen Formation were dominated by infaunal bivalves and deep-shelf assemblages of the Swabian Alb by pedunculate brachiopods.

Vellerat, Balsthal and Villigen formations. The compositional segregation between the deep-shelf Villigen Formation with soft-bottom habitats dominated by shallow burrowing bivalves, and the platform-like Vellerat and Balsthal formations with mixed-bottom habitats dominated by brachiopods and epifaunal bivalves might by affected by absence of samples from oolitic and coral deposits of the Holzflue and Olten members that formed the margin of the Swiss Jura Platform (Gygi, 1990a). This segregation can also be related to discontinuous nature of environments between platform and deep shelf, leading to poor compositional gradation between benthic communities. The most parsimonious explanations for the increasing abundance of infaunal bivalves with increasing depth can be related to decreasing substrate consistency that can be unfavourable for epifaunal bivalves and brachiopods. However, the Villigen Formation with bivalves locally contains dispersed siliceous sponges that can locally form small-scale mounds in the Crenularis Member and the Knollen Bed, implyingsome availability of hard substrates in the deep shelf of the Swiss Jura. In addition, within the Villigen Formation, high rate of sedimentation of carbonate mud exported from the Swiss Jura Platform might negatively affect abundance of infaunal suspension-feeding bivalves and other organisms. Pittet and Strasser (1998b) observed that abundance of benthic macrofossils in the Oxfordian of the eastern Swiss Jura and southern Germany positively correlates with glauconite content and intensity of bioturbation. Infaunal bivalves of the Villigen Formation are typically bounded to beds that show higher proportions of signs of oncoidal crusts and glauconite than shell-poor beds. Reduced abundance of infaunal bivalves and other benthic fauna in shell-poor mudstones and wackestones of the Villigen Formation can thus indicate that very high sedimentation rates were also inhibitive for infaunal bivalves.

The carbonate-dominated deep shelf of the eastern Swiss Jura graded to the east into sponge-dominated shelf of southern Germany that was affected by higher supply of terrigenous material (Impressamergel Formation). However, in contrast to the Villigen Formation, the guild structure is completely different, being dominated by pedunculate brachiopods in sponge biostromes and mounds. Soft-bottom habitats in the vicinity of mounds contain small-sized brachiopods and rare shallow-burrowing deposit-feeding bivalves. The comparison of species composition of the Swiss Jura Platform and the Swabian Basin in the *Epipeltoceras bimammatum* Zone is shown in Figure 16. The distance between carbonate-rich habitats of the Villigen Formation (Villigen-Geissberg section) and mixed, siliciclastic-carbonate habitats of the Impressamergel Formation (Gosheim section) is only about 100 km. Note that both sections reflect low-energy habitats that originated below storm wave base. Rarity of infaunal suspension-feeding bivalves in soft-bottom habitats of the Impressamergel Formation can be related to restricted circulation patterns in southern Germany owing to its lower connection with the open Tethys ocean when compared to the Swiss Jura environments. This effect might have caused lower current activity and lower oxygen levels in southern Germany that probably limited abundance of infaunal suspension-feeding bivalves. This idea is supported by abundance of *Chondrites* burrows in dark marls of the Impressamergel Formation, and abundance of microbial crusts in sponge mounds that can be indicative of oxygen-deficient conditions (Leinfelder, 2001). Reduced food supply probably does not account for the rarity of infaunal bivalves in the epicontinental sea of southern Germany because this region was similarly close or closer to siliciclastic sources of the Rhenish Massif as the Swiss Jura Platform during the Late Jurassic.

Conclusions

(1) During the Early and early Middle Oxfordian, infaunal bivalves dominated in soft-bottom, terrigenous-rich habitats, and epibyssate and cementing bivalves were most abundant in hard-bottom, carbonate-rich habitats with corals in the western part of the Swiss Jura. Brachiopod species were abundant in marl-rich soft-bottom and carbonate-rich hard-bottom habitats, implying pronounced tolerances of brachiopods with respect to varying siliciclastic supply, with the rhynchonellid *Thurmanella* being especially well adapted to soft-bottom habitats rich in terrigenous supply.

(2) During the Late Oxfordian, benthic communities of the Swiss Jura deep shelf dominated by infaunal bivalves contrast with sponge-dominated benthic communities with brachiopods that were typical of deep shelf of southern Germany. In the Swiss Jura, cementing bivalves and brachiopods dominated in shallow, mixed-bottom habitats on the platform, and infaunal suspension-feeding bivalves were abundant in deep-shelf, soft-bottom habitats. Abundance of infaunal bivalves in offshore, carbonate-rich deposits of the Swiss Jura thus contrasts with their rarity in offshore soft-bottom habitats of southern Germany. Rarity of infaunal bivalves in the Swabian-Franconian epicontinental sea during Late Oxfordian was probably not owing to the scarcity of land-derived

nutrients because this region was similarly close or closer to siliciclastic sources of the Rhenish Massif than the Swiss Jura Platform. Instead, the abundance of infaunal bivalves in the Swiss Jura can be more related to conditions with good oxygenation near platform margin, in contrast to *Chondrites*-rich marls and limestones of southern Germany characterized by reduced flow velovity and reduced oxygen levels.

	H25	H26	H27	H28	E1	E2	LI1-1	LI1-2	LI1-8	LI1-10	LI1-17.4	LI1-65	LI1-66	LI1-85	LI2-85	LI2-94	BV3	BV6	BV2
Septaliphoria arduennensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella arolica	3	17	0	3	1	14	0	0	0	0	0	0	0	0	0	0	0	0	0
Thurmanella obtrita	0	0	0	0	0	0	20	8	6	4	52	28	25	10	8	28	19	0	0
Monticlarella triloboides	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Argovithyris birmensdorfensis	34	106	25	121	35	13	0	0	0	0	0	0	0	0	0	0	0	0	0
Placothyris rollieri	0	5	0	7	16	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Loboidothyris zieteni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aromasithyris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galliennithyris gallienei	0	0	0	0	0	0	0	26	11	24	0	0	0	29	33	2	0	0	0
Gallienithyris bourguetti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gallienithyris elliptoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucleata nucleata	3	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonellina loricata	0	23	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina orbis	1	13	19	34	3	4	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria astartina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Digonella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ornithella (Delmontanella) delmontana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praesaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3
Rollieria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Dacryomya sp.	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
Barbatia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp.	0	0	0	0	0	0	0	1	3	3	0	2	0	0	0	0	0	0	3
Grammatodon (Cosmetodon) sp.	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arca sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. A	0	4	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. B	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eonavicula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus bipartitus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Bakevellia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	1	0	0
Meleagrinella sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Inoceramid	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Radulopecten strictus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Radulopecten fibrosus	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Spondylopecten sp.	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Spondylopecten (Plesiopecten) sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Chlamys (Chlamys) textoria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camptonectes (Camptonectes) auritus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium (E.) corneolum	0	0	0	0	0	0	1	3	0	2	0	0	0	1	0	1	3	25	4
Plagiostoma sp. F	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudolimea sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudolimea sp. B	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	2	0	6
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Acesta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Atreta sp.	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nanogyra nana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Liostrea sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lucinid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myoconcha sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Myophorella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella (Trautscholdia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Nicaniella (Nicaniella) extensa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corbulomima sp.	0	0	0	0	0	0	2	1	3	0	0	0	0	0	0	0	0	0	6
Coeloastarte sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcticid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astartid indet	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eocallista sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opis (Trigonopis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	29
Protocardia (Protocardia) intexta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) dyonisea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anisocardia sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anisocardia sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isocyprina sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neocrasina sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Integricardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unicardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Heterodont indet	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Bucardiomya) protei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
Pachymya (Arcomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cercomya undulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Goniomya literata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pholadomya (Pholadomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya uniformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya alduini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Homomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anomalodesmatan indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Supplement 1 – Absolute abundanes of brachiopods and bivalves.

	BV4	BV5	LI2-1	LI2-2	LI2-3	LI2-4	PR1	PR2	PR4	PR5	PR7	CV1	CV2	CV3	CV4	CV6	CV7	LQ1	LQ2
Septaliphoria arduennensis	0	0	0	0	0	0	0	0	0	0	0	14	8	1	3	1	2	1	0
Lacunosella arolica	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Thurmanella obtrita	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Monticlarella triloboides	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Argovithyris birmensdorfensis	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Placothyris rollieri	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Loboidothyris zieteni	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Aromasithyris sp.	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Galliennithyris gallienei	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Gallienithyris bourguetti	3	2	0	0	2	2	7	4	5	10	10	*0*	0	0	0	0	0	0	0
Gallienithyris elliptoides	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Nucleata nucleata	0	0	0	0	0	0	0	0	0	0	0	*0*	0	0	0	0	0	0	0
Trigonellina loricata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina orbis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria astartina	0	0	0	0	0	0	0	0	0	0	0	65	21	4	58	1	1	15	5
Digonella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ornithella (Delmontanella) delmontana	7	1	3	0	5	2	27	16	32	12	14	0	0	0	0	0	0	0	0
Nuculoma sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praesaccella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Rollieria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dacryomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Barbatia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammatodon (Grammatodon) sp.	0	0	0	1	0	0	0	0	0	0	0	0	1	0	5	0	0	0	0
Grammatodon (Cosmetodon) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arca sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. B	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Eonavicula sp.	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Arcomytilus sp.	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	2	1
Modiolus sp.	0	0	0	0	0	0	0	0	0	0	0	1	4	0	0	0	0	0	0
Modiolus bipartitus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gervillella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bakevellia sp.	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Oxytoma sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meleagrinella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoceramid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Ctenostreon sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Radulopecten strictus	0	0	0	0	0	0	0	0	0	0	3	25	19	0	25	22	0	0	0
Radulopecten fibrosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spondylopecten sp.	0	0	0	0	0	0	0	0	6	0	1	0	0	0	0	0	0	0	0
Spondylopecten (Plesiopecten) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys (Chlamys) textoria	17	20	18	14	8	3	1	4	1	1	1	0	0	0	0	0	0	1	0
Camptonectes (Camptonectes) auritus	3	0	0	1	0	0	0	1	0	3	0	2	0	0	0	0	0	0	0
Entolium (E.) corneolum	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	3	0	0
Plagiostoma sp. F	0	3	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudolimea sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudolimea sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acesta sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Atreta sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Actinostreon gregareum	0	1	0	1	0	1	0	0	0	0	0	0	13	0	0	2	0	0	1
Nanogyra nana	12	6	0	1	1	1	0	0	0	0	0	14	16	17	17	31	19	59	22
Liostrea sp.	2	3	2	4	6	16	0	0	0	0	0	1	0	18	0	2	0	3	2
Lucinid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Myoconcha sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonia (Trigonia) sp.	0	0	0	0	0	0	0	0	0	0	0	1	2	0	2	0	0	1	0
Myophorella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Nicaniella (Trautscholdia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella (Nicaniella) extensa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corbulomima sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Coeloastarte sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcticid indet	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Astartid indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eocallista sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Opis (Trigonopis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Protocardia (Protocardia) sp.	0	0	0	1	0	0	0	0	1	0	0	2	3	0	4	2	0	0	0
Protocardia (Protocardia) intexta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) dyonisea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anisocardia sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0
Anisocardia sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isocyprina sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neocrasina sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Integricardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unicardium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thracia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heterodont indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
Pholadomya (Bucardiomya) protei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachymya (Arcomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cercomya undulata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Goniomya literata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pholadomya (Pholadomya) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pleuromya uniformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pleuromya alduini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Homomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Anomalodesmatan indet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0

Supplement 1 (cont.) - Absolute abundanes of brachiopods and bivalves.

	LQ3	LQ4	GP2	GP1	GP3	V1	V2	V3	V6	V7	V8	V10	V11
Septaliphoria arduennensis	2	4	4	7	2	0	0	0	0	0	0	0	0
Lacunosella arolica	0	0	0	0	0	0	0	0	0	0	0	0	0
Thurmanella obtrita	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella triloboides	0	0	0	0	0	0	0	0	0	0	0	0	0
Argovithyris birmensdorfensis	0	0	0	0	0	0	0	0	0	0	0	0	0
Placothyris rollieri	0	0	0	0	0	0	0	0	0	0	0	0	0
Loboidothyris zieteni	0	0	0	0	2	0	0	0	0	0	0	0	0
Aromasithyris sp.	0	0	0	0	0	0	0	0	4	0	0	7	8
Galliennithyris gallienei	0	0	0	0	0	0	0	0	0	0	0	0	0
Gallienithyris bourguetti	0	0	0	0	0	0	0	0	0	0	0	0	0
Gallienithyris elliptoides	1	0	0	0	0	0	0	0	0	0	0	0	0
Nucleata nucleata	0	0	0	0	0	0	0	0	0	0	0	0	0
Trigonellina loricata	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina orbis	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria astartina	8	24	22	10	9	0	0	0	0	0	0	0	0
Digonella sp.	0	0	0	0	0	0	0	0	0	0	0	3	0
Ornithella (Delmontanella) delmontana	0	0	0	0	0	0	0	0	0	0	0	0	0
Nuculoma sp.	0	0	0	0	0	2	0	0	0	0	0	0	0
Praesaccella sp.	0	0	0	0	0	0	2	2	0	0	0	0	0
Palaeonucula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesosaccella sp.	0	0	0	0	0	1	0	0	0	0	0	0	0
Rollieria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Dacryomya sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Barbatia sp.	0	0	0	0	0	0	0	0	0	0	0	1	0
Grammatodon (Grammatodon) sp.	0	0	1	0	0	7	6	3	0	2	6	2	0
Grammatodon (Cosmetodon) sp.	0	0	0	0	0	0	0	0	0	0	0	1	2
Arca sp. A	0	0	1	0	0	0	0	0	0	0	0	0	0
Isoarca sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoarca sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0
Eonavicula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcomytilus sp.	1	0	4	0	0	0	0	0	0	0	0	0	0
Modiolus sp.	0	0	0	1	0	0	0	0	0	0	0	0	0
Modiolus bipartitus	0	0	0	0	0	0	0	0	12	0	0	0	0
Gervillella sp.	0	1	0	0	0	0	0	0	4	1	0	0	0
Bakevellia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma sp.	1	0	0	0	0	0	0	0	0	0	0	1	0
Meleagrinella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoceramid	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinna sp.	0	0	0	0	0	0	0	0	0	0	0	0	2
Ctenostreon sp.	0	0	1	0	0	0	0	0	0	0	0	0	0
Eopecten sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Radulopecten strictus	0	0	21	5	0	0	0	0	0	0	0	0	0
Radulopecten fibrosus	0	0	0	0	0	0	0	0	0	0	0	0	0
Spondylopecten sp.	0	0	0	0	0	0	0	0	0	3	0	0	0
Spondylopecten (Plesiopecten) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys (Chlamys) textoria	0	0	0	0	1	0	0	0	1	0	0	12	2
Camptonectes (Camptonectes) auritus	0	0	1	0	0	0	0	0	0	0	0	0	0
Entolium (E.) corneolum	0	0	0	7	0	0	0	0	0	3	6	4	7
Plagiostoma sp. F	0	0	1	0	1	0	0	0	0	0	0	1	0
Pseudolimea sp. A	0	0	0	1	0	0	0	0	0	0	0	1	0
Pseudolimea sp. B	0	0	0	0	0	0	0	0	0	0	0	0	0
Limatula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Acesta sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Atreta sp.	0	0	0	0	0	0	0	0	0	0	0	0	1
Plicatula sp.	0	0	0	0	0	0	0	0	0	0	0	1	0
Placunopsis sp.	0	0	0	0	0	0	0	0	0	1	1	0	0
Actinostreon gregareum	0	0	0	0	5	0	0	0	0	0	0	0	0
Nanogyra nana	28	16	70	21	13	0	0	0	0	0	0	0	0
Liostrea sp.	0	0	7	0	12	0	0	0	5	1	1	0	1
Lucinid indet	0	0	0	0	0	0	0	0	0	0	0	0	0
Myoconcha sp.	0	0	0	0	0	0	0	0	0	0	0	0	1
Trigonia (Trigonia) sp.	0	0	0	0	0	0	0	0	1	1	0	0	1
Myophorella sp.	0	0	0	0	0	0	2	0	0	0	0	0	0
Nicaniella (Trautscholdia) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Nicaniella (Nicaniella) extensa	0	0	0	0	0	12	50	17	1	0	4	0	0
Corbulomima sp.	0	0	0	0	0	2	0	1	0	0	0	0	0
Coeloastarte sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcticid indet	0	0	0	0	0	0	0	0	0	0	0	0	0
Astartid indet	0	0	0	0	0	0	0	0	0	0	0	0	0
Eocallista sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Opis (Trigonopis) sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) sp.	1	0	5	3	0	0	0	0	0	0	0	0	0
Protocardia (Protocardia) intexta	0	0	0	0	0	2	1	3	8	1	4	0	3
Protocardia (Protocardia) dyonisea	0	0	0	0	0	0	2	0	0	0	0	0	0
Anisocardia sp. A	0	0	1	0	0	0	0	0	2	1	2	0	0
Anisocardia sp. B	0	0	0	3	0	0	0	0	0	0	0	0	0
Isocyprina sp.	0	0	0	0	0	2	0	0	0	0	0	1	0
Neocrasina sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Integricardium sp.	0	0	0	0	0	1	0	0	0	3	0	0	0
Unicardium sp.	0	0	0	0	0	0	0	0	0	0	4	0	0
Thracia sp.	0	0	0	0	0	0	1	0	0	0	0	0	0
Heterodont indet	0	0	0	0	0	4	0	0	0	0	3	0	0
Pholadomya (Bucardiomya) protei	0	0	0	0	0	0	0	1	13	2	0	0	0
Pachymya (Arcomya) sp.	0	0	0	0	1	0	0	0	0	0	0	0	0
Cercomya undulata	0	0	0	0	0	0	1	1	0	2	0	0	0
Goniomya literata	0	0	0	0	0	0	0	0	9	1	0	0	1
Pholadomya (Pholadomya) sp.	0	0	0	0	0	0	0	1	0	2	0	0	0
Pleuromya uniformis	0	0	0	0	0	0	0	0	1	2	0	0	0
Pleuromya alduini	0	0	0	0	0	0	0	0	0	0	1	0	1
Homomya sp.	0	2	0	0	0	0	0	0	0	0	0	0	0
Anomalodesmatan indet	0	0	0	0	0	0	0	0	0	0	0	1	0

Supplement 1 (cont.) - Absolute abundanes of brachiopods and bivalves.

Species	Guild
Septaliphoria arduennensis	pedunculate brachiopod
Lacunosella arolica	pedunculate brachiopod
Thurmanella obtrita	pedunculate brachiopod
Monticlarella triloboides	pedunculate brachiopod
Argovithyris birmensdorfensis	pedunculate brachiopod
Placothyris rollieri	pedunculate brachiopod
Loboidothyris zieteni	pedunculate brachiopod
Aromasothyris sp.	pedunculate brachiopod
Galliennithyris gallienei	pedunculate brachiopod
Gallienithyris bourguetti	pedunculate brachiopod
Gallienithyris elliptoides	pedunculate brachiopod
Nucleata nucleata	pedunculate brachiopod
Trigonellina loricata	pedunculate brachiopod
Zittelina orbis	pedunculate brachiopod
Zeilleria astartina	pedunculate brachiopod
Digonella sp.	pedunculate brachiopod
Ornithella (Delmontanella) delmontana	pedunculate brachiopod
Nuculoma sp.	shallow burrowing protobranch
Praesaccella sp.	shallow burrowing protobranch
Palaeonucula sp.	shallow burrowing protobranch
Mesosaccella sp.	shallow burrowing protobranch
Rollieria sp.	shallow burrowing protobranch
Dacryomya sp.	shallow burrowing protobranch
Barbatia sp.	epibyssate filibranch
Grammatodon (Grammatodon) sp.	epibyssate filibranch
Grammatodon (Cosmetodon) sp.	endobyssate filibranch
Arca sp. A	epibyssate filibranch
Isoarca sp. A	shallow burrowing protobranch
Isoarca sp. B	shallow burrowing protobranch
Eonavicula sp.	epibyssate filibranch
Arcomytilus sp.	epibyssate filibranch
Modiolus sp.	endobyssate filibranch
Modiolus bipartitus	endobyssate filibranch
Gervillella sp.	endobyssate filibranch
Bakevellia sp.	epibyssate filibranch
Oxytoma sp.	epibyssate filibranch
Meleagrinella sp.	epibyssate filibranch
Pteria sp.	epibyssate filibranch
Inoceramid	epibyssate filibranch
Pinna sp.	endobyssate filibranch
Ctenostreon sp.	epibyssate filibranch
Eopecten sp.	epibyssate filibranch
Radulopecten strictus	epibyssate filibranch
Radulopecten fibrosus	epibyssate filibranch
Spondylopecten sp.	epibyssate filibranch
Spondylopecten (Plesiopecten) sp.	epibyssate filibranch
Chlamys (Chlamys) textoria	epibyssate filibranch
Camptonectes (Camptonectes) auritus	epibyssate filibranch
Entolium (E.) corneolum	free-lying filibranch
Entolium (Cingentolium) sp.	free-lying filibranch
Plagiostoma sp. F	epibyssate filibranch
Pseudolimea sp. A	epibyssate filibranch
Pseudolimea sp. B	epibyssate filibranch
Limatula sp.	epibyssate filibranch
Acesta sp.	epibyssate filibranch
Atreta sp.	cementing filibranch
Plicatula sp.	cementing filibranch
Placunopsis sp.	cementing filibranch
Actinostreon gregareum	cementing pseudolamellibranch
Nanogyra nana	cementing pseudolamellibranch
Liostrea sp.	cementing pseudolamellibranch
Lucinid indet	shallow burrowing chemosymbiont
Myoconcha sp.	shallow burrowing filibranch
Trigonia (Trigonia) sp.	shallow burrowing filibranch
Myophorella sp.	shallow burrowing filibranch
Nicaniella (Trautscholdia) sp.	shallow burrowing eulamellibranch
Nicaniella (Nicaniella) extensa	shallow burrowing eulamellibranch
Corbulomima sp.	shallow burrowing eulamellibranch
Coeloastarte sp.	shallow burrowing eulamellibranch
Arcticid indet	shallow burrowing eulamellibranch
Astartid indet	shallow burrowing eulamellibranch
Eocallista sp.	shallow burrowing eulamellibranch
Opis (Trigonopis) sp.	shallow burrowing eulamellibranch
Protocardia (Protocardia) sp.	shallow burrowing eulamellibranch
Protocardia (Protocardia) intexta	shallow burrowing eulamellibranch
Protocardia (Protocardia) dyonisea	shallow burrowing eulamellibranch
Anisocardia sp. A	shallow burrowing eulamellibranch
Anisocardia sp. B	shallow burrowing eulamellibranch

Supplement 2 – Guild assignments of brachiopods and bivalves

Species	Guild
Isocyprina sp.	shallow burrowing eulamellibranch
Neocrasina sp.	shallow burrowing eulamellibranch
Integricardium sp.	shallow burrowing eulamellibranch
Unicardium sp.	shallow burrowing eulamellibranch
Thracia sp.	deep burrowing eulamellibranch
Heterodont indet	shallow burrowing eulamellibranch
Pholadomya (Bucardiomya) sp.	deep burrowing eulamellibranch
Pholadomya (Bucardiomya) protei	deep burrowing eulamellibranch
Pachymya (Arcomya) sp.	deep burrowing eulamellibranch
Cercomya sp.	deep burrowing eulamellibranch
Cercomya undulata	deep burrowing eulamellibranch
Goniomya literata	deep burrowing eulamellibranch
Pholadomya (Pholadomya) sp.	deep burrowing eulamellibranch
Pleuromya uniformis	deep burrowing eulamellibranch
Pleuromya alduini	deep burrowing eulamellibranch
Homomya sp.	deep burrowing eulamellibranch
Anomalodesmatan indet	deep burrowing eulamellibranch

Supplement 2 (cont.) - Guild assignments of brachiopods and bivalves

Sample	Zone	Member	Siliciclastic	Substrate	Wave-base level
Holderbank 25	*G. transversarium*	Birmenstorf Member	marly limestone	Mixed-bottom	Below MSWB
Holderbank 26	*G. transversarium*	Birmenstorf Member	marly limestone	Mixed-bottom	Below MSWB
Holderbank 27	*G. transversarium*	Birmenstorf Member	marly limestone	Mixed-bottom	Below MSWB
Holderbank 28	*G. transversarium*	Birmenstorf Member	marly limestone	Mixed-bottom	Below MSWB
Eisenberg 1	*G. transversarium*	Birmenstorf Member	marly limestone	Mixed-bottom	Below MSWB
Eisenberg 2	*G. transversarium*	Birmenstorf Member	marly limestone	Mixed-bottom	Below MSWB
Liesberg 1-1	*C. cordatum* Zone	Sornetan Member	siltstone	Soft-bottom	Below MSWB
Liesberg 1-2	*C. cordatum* Zone	Sornetan Member	silty marlstone	Soft-bottom	Below MSWB
Liesberg 1-8	*C. cordatum* Zone	Sornetan Member	silty marlstone	Soft-bottom	Below MSWB
Liesberg 1-10	*C. cordatum* Zone	Sornetan Member	silty marlstone	Soft-bottom	Below MSWB
Liesberg 1-17.4	*C. cordatum* Zone	Sornetan Member	silty marlstone	Soft-bottom	Below MSWB
Liesberg 1-65	*G. transversarium*	Sornetan Member	siltstone	Soft-bottom	Below MSWB
Liesberg 1-66	*G. transversarium*	Sornetan Member	silty marlstone	Soft-bottom	Below MSWB
Liesberg 1-85	*G. transversarium*	Sornetan Member	silty marlstone	Soft-bottom	Below MSWB
Liesberg 2-85	*G. transversarium*	Sornetan Member	silty marlstone	Soft-bottom	Below MSWB
Liesberg 1-94	*G. transversarium*	Sornetan Member	silty marlstone	Soft-bottom	Below MSWB
Barschwill-Vogeli 3	*G. transversarium*	Sornetan Member	siltstone	Soft-bottom	Below MSWB
Barschwill-Vogeli 6	*G. transversarium*	Sornetan Member	siltstone	Soft-bottom	Below MSWB
Barschwill-Vogeli 2	*G. transversarium*	Sornetan Member	siltstone	Soft-bottom	Below MSWB
Barschwill-Vogeli 4	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above MSWB
Barschwill-Vogeli 5	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above MSWB
Liesberg 2-1	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above MSWB
Liesberg 2-2	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above MSWB
Liesberg 2-3	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above MSWB
Liesberg 2-4	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above MSWB
Peute Roche-Vellerat 1	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above MSWB
Peute Roche-Vellerat 2	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above MSWB
Peute Roche-Vellerat 4	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above MSWB
Peute Roche-Vellerat 5	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above NSWB
Peute Roche-Vellerat 7	*G. transversarium*	Liesberg Member	marly limestone	Hard-bottom	Above NSWB
Chapel Vorlbourg-Delemont 1	*E. bimammatum*	Bure Member	limestone	Mixed-bottom	Above MSWB
Chapel Vorlbourg-Delemont 2	*E. bimammatum*	Bure Member	limestone	Mixed-bottom	Above MSWB
Chapel Vorlbourg-Delemont 3	*E. bimammatum*	Bure Member	marly limestone	Mixed-bottom	Above NSWB
Chapel Vorlbourg-Delemont 4	*E. bimammatum*	Bure Member	marly limestone	Mixed-bottom	Above NSWB
Chapel Vorlbourg-Delemont 6	*E. bimammatum*	Bure Member	limestone	Mixed-bottom	Above MSWB
Chapel Vorlbourg-Delemont 7	*E. bimammatum*	Bure Member	limestone	Mixed-bottom	Above MSWB
Liesberg quarry 1	*E. bimammatum*	Laufen Member	limestone	Mixed-bottom	Above NSWB
Liesberg quarry 2	*E. bimammatum*	Laufen Member	limestone	Mixed-bottom	Above NSWB
Liesberg quarry 3	*E. bimammatum*	Laufen Member	limestone	Mixed-bottom	Above NSWB
Liesberg quarry 4	*E. bimammatum*	Laufen Member	limestone	Mixed-bottom	Above NSWB
Pichoux gorge 2	*E. bimammatum*	Laufen Member	limestone	Mixed-bottom	Above MSWB
Pichoux gorge 1	*E. bimammatum*	Laufen Member	limestone	Mixed-bottom	Above MSWB
Pichoux gorge 3	*E. bimammatum*	Laufen Member	limestone	Mixed-bottom	Above MSWB
Villingen-Geisberg 1	*E. bimammatum*	Geissberg Member	limestone	Soft-bottom	Below MSWB
Villingen-Geisberg 2	*E. bimammatum*	Geissberg Member	limestone	Soft-bottom	Below MSWB
Villingen-Geisberg 3	*E. bimammatum*	Geissberg Member	limestone	Soft-bottom	Below MSWB
Villingen-Geisberg 6	*E. bimammatum*	Crenularis Member	limestone	Mixed-bottom	Below MSWB
Villingen-Geisberg 7	*E. bimammatum*	Crenularis Member	limestone	Mixed-bottom	Below MSWB
Villingen-Geisberg 8	*E. bimammatum*	Wangen Member	limestone	Soft-bottom	Below MSWB
Villingen-Geisberg 10	*E. bimammatum*	Wangen Member	limestone	Mixed-bottom	Below MSWB

Supplement 3 – Stratigraphic and environmental assignments.

12. Dominance of brachiopods on a pelagic carbonate platform (Pieniny Klippen Belt, West Carpathians): effects of substrate, bottom currents and food supply

(with Ján Schlögl and Marián Golej)

Abstract. Level-bottom benthic communities inhabiting the Middle Jurassic-earliest Cretaceous pelagic carbonate platforms of the Czorsztyn swell (Pieniny Klippen Belt, West Carpathians) were dominated by pedunculate brachiopods and characterized by a distinctive guild structure with common epifaunal and rare or absent semi-infaunal and infaunal bivalves. Although micritic deposits show extensive signs of aragonite dissolution, a strong taphonomic bias against less durable infaunal bivalves can be excluded because ammonite concentrations with rare signs of dissolution are similarly dominated by brachiopods and epifaunal bivalves. In spite of a substantial temporal taxonomic turnover, this guild structure was constant in time and was typical also of other Jurassic pelagic platforms of the western Tethys. Rarity of infaunal bivalves on the pelagic platforms can be explained by increased substrate firmness due to combined effects of reduced sedimentation rates, aragonite dissolution and rapid calcite cementation. Brachiopods and bivalves significantly differ in their abundance patterns. Brachiopod abundance decreased and bivalve abundance increased towards habitats with higher intensity of bottom currents on the scale of the Czorsztyn pelagic platform. Basin-scale qualitative data indicate that abundance of brachiopods and bivalves increased from deep sea to pelagic platform in the Pieniny Klippen Belt Basin (PKBB), although terebratulid brachiopods were able to inhabit deep-sea habitats. The platform-scale and PKBB-scale distribution patterns thus show that brachiopods preferred deeper or lower-energy habitats with lower particulate flux than epifaunal bivalves. The abundance of brachiopods in deeper parts of the Jurassic pelagic platforms might be explained by combined effects of firm substrate and better exploitation of depleted food in sluggish flows when compared to epifaunal bivalves. It is suggested that the success of brachiopods on the shallow Jurassic intra-oceanic pelagic platforms was related to unique abiotic conditions rather than to selective extinction of shallow-water incumbents and subsequent colonization of shallow habitats by deep-sea brachiopods.

Introduction

During the Jurassic, one of the most common habitats of brachiopods were sediment-starved pelagic carbonate platforms or swells in the westerly-closed Tethys Ocean (Garrison and Fisher, 1969; Jenkyns, 1971; Santantonio, 1993). For example, brachiopods dominated over epifaunal bivalves in such habitats during the Early Jurassic in the Alps (Böhm et al. 1999; Vörös et al., 2003), Carpathians (Siblík, 1966), Transdanubian Central Range (Vörös, 1986; Dulai, 2003), during the Middle Jurassic in the Carpathians (Mišík et al., 1994; Wierzbowski et al., 1999), Transdanubian Central Range (Vörös, 1995), Eastern Alps (Oppel, 1863), Southern Alps (Sturani, 1971; Benigni et al., 1982) and western Sicily (Wendt, 1971) and during the Late Jurassic in the Carpathians (Siblík, 1979; Barczyk, 1979, 1991; Krobicki, 1994), Transdanubian Central Range (Fözy et al., 1994; Kázmér, 1998) and Southern Alps (Dieni and Middlemiss, 1981).

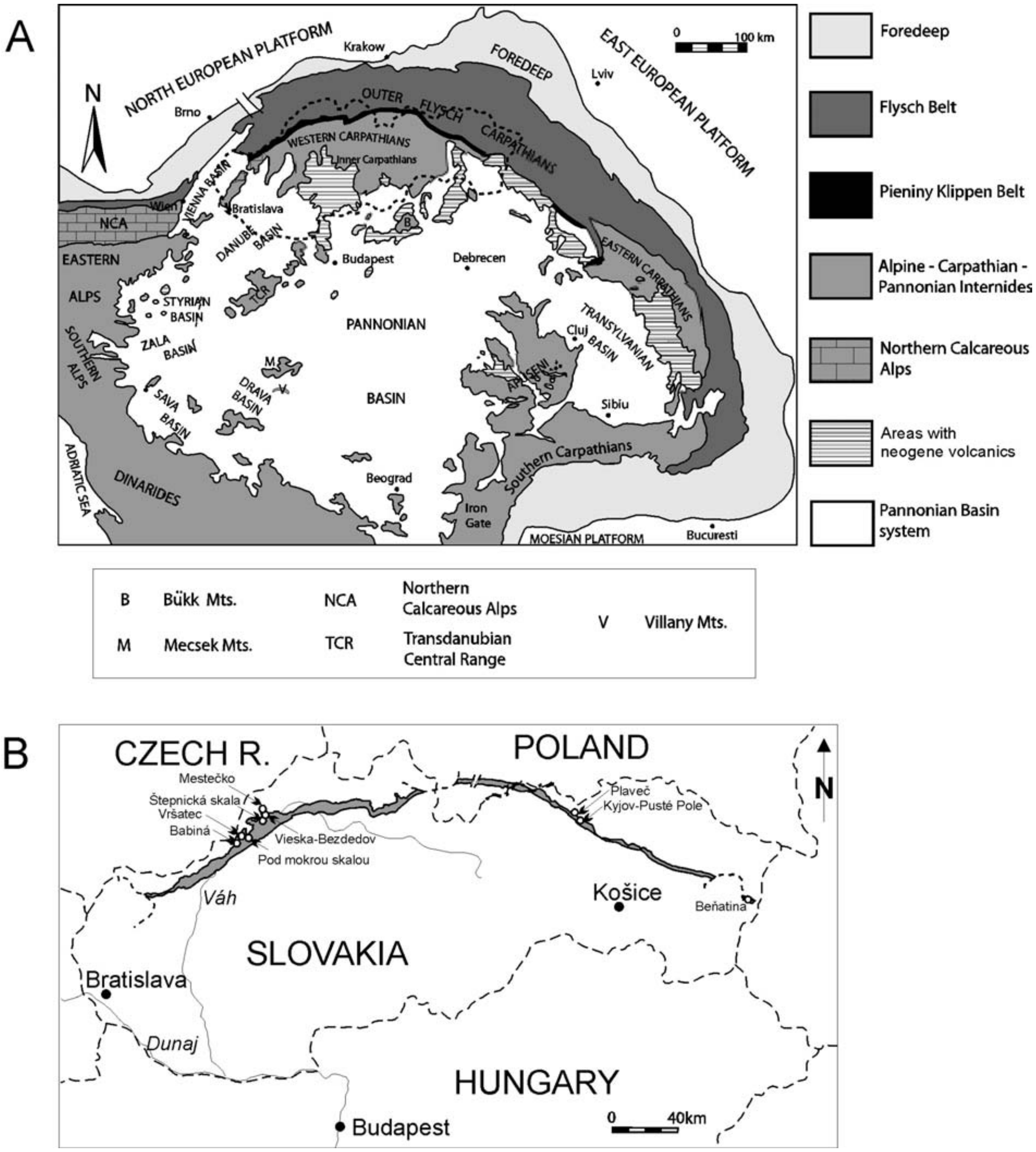


Figure 1 – A. Geologic location of the Pieniny Klippen Belt in the West Carpathians and its relationship to other paleotectonic units. B. Geographic location of the sections within the Middle Jurassic-lowermost Cretaceous successions of the Czorsztyn unit (Pieniny Klippen Belt) in the West Carpathians.

Ancient pelagic carbonate platforms can be compared with respect to benthic ecosystems to present-day seamounts. Seamounts represent specific habitats because of the topographically-enhanced currents in their vicinity that enhance particulate flux in the otherwise food-poor deep sea. Present-day seamounts are mostly of volcanic origin and are strictly defined as structures elevated more than 1000 m above the sea-floor and of limited areal extent at their top (Rogers, 1994). Seamounts commonly harbour dense aggregations of suspension-feeders, including brachiopods (Richer de Forges et al., 2000; Gaspard, 2003). Seamount benthos seems to be dominated by endemic, long-lived and slow-growing taxa (Koslow et al., 2001). Jurassic pelagic platforms might provide one of the important habitats for the radiation of brachiopods because Mesozoic brachiopods reached their peak in terms of community-level abundance and taxonomic diversity during the Jurassic (Ager, 1965; Williams and Hurst, 1977; Aberhan, 1994; Vörös, 2005). In spite of this, abiotic and biotic factors that allowed brachiopod success on the Jurassic pelagic carbonate platforms are poorly known.

The main goal of this chapter is to distinguish the possible causes of brachiopod dominance and success on pelagic carbonate platforms in the western Tethys. The aim is to describe benthic communities with brachiopod and bivalves from the Czorsztyn pelagic platform of the Pieniny Klippen Belt Basin (PKBB), to assess their co-occurrence in terms of their abundance patterns, to analyse their environmental distribution and to discuss possible taphonomic biases that may cause a difference between real and observed community structure.

Pieniny Klippen Belt Basin during the Middle Jurassic-earliest Cretaceous

The pelagic platforms in the western Tethys were characterized by deposition of carbonate deposits with minor thickness, minor siliciclastic admixture, signs of substantial condensation and synsedimentary tectonics. In the West Carpathians (Fig. 1), one of the examples with brachiopod communities occurring in such environments is represented by the Middle and Upper Jurassic deposits of the Czorsztyn Unit. This unit structurally belongs to the Pieniny Klippen Belt and records one of its shallowest successions. The Czorsztyn Unit presently represents an about 20 km wide and 500 km long relict of a pelagic carbonate platform that was bordered on both margins by basins with deep-water sediments (Fig. 2, Mišík, 1993; 1997). This ridge is a relict of an extensive Triassic carbonate-siliciclastic shelf, which was (1) disintegrated into fragments during the Middle Jurassic extensional tectonic activity related to the opening of the PKBB and the Ligurian-Piedmont Ocean, and (2) affected by tilting and differential subsidence of the fault-controlled blocks (e.g., Krobicki, 1996; Golonka and Krobicki, 2001).The pelagic carbonate platform of the Czorsztyn Unit probably originated at the beginning of Bajocian (Aubrecht et al., 1997), leading to the main bathymetric differentiation of the PKBB into basin and pelagic platform.

Several depositional units with distinct Middle Jurassic-Lower Cretaceous lithostratigraphic successions have been distinguished within the PKBB. These units were interpreted as representing parts of a simplified, approximately N-S oriented transect that dissects the PKBB into discrete bathymetric environments (Fig. 2, Birkenmajer, 1977, 1986; Wierzbowski et al., 2004). The axial, deepest part of the PKBB was represented by radiolarites and plankton-dominated limestone deposits of the Branisko and Pieniny units. The platform-basin transition was formed by radiolarite-rich successions of the Czertezik and Pruské (Niedzica) units on the northern side of the PKBB. The carbonate platform belonging to the Czorsztyn Unit was dissected into fault-controlled blocks. The blocks can be differentiated into shallower environments with crinoidal limestones, breccia and shell beds and deeper environments dominated by red nodular limestones. The Czorsztyn Unit was bordered by the Magura Basin on its northern side, with deposits similar to those of the Pieniny Unit.

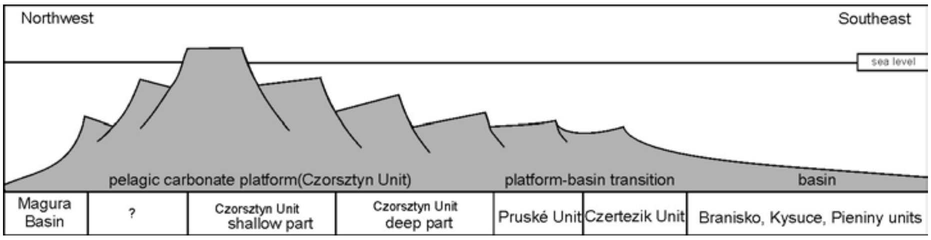


Figure 2 - Simplified N-S oriented bathymetric transect through the Pieniny Klippen Belt.

Pelagic platform. During the Bajocian, white crinoidal grainstones of the Smolegowa Formation and red crinoidal packstones of the Krupianka Formation were deposited in the Czorsztyn Unit (Fig. 3). Clasts of crinoidal and bioclastic limestones of the Krasín Breccia (Bajocian) with signs of multiple reworking, complex cements and complex sediment infillings were deposited on the foot-walls of the fault-blocks. Coral framestones and floatstones of the Vršatec Formation that locally occur in the western part of the PKB probably originated on elevated parts of the fault-blocks (Fig. 3). Although the Vršatec Formation was assigned to the Oxfordian (Mišík, 1979; Morycowa and Mišík, 2005), its stratigraphic position was misinterpreted because this formation contains Bajocian-Bathonian ammonites and is overlain by crinoidal limestones with Bajocian-Bathonian brachiopods (Schlögl and Tomašových, unpublished). Red, nodular or poorly nodular, micrite-rich limestones of the Czorsztyn Formation began their deposition at the Bajocian/Bathonian boundary (Fig. 3). Since the Bathonian, the depth of the Czorsztyn Unit was probably below the photic zone because of total absence of benthic green algae, zooxanthellate corals and shallow-water benthic foraminifers that were typical of coeval carbonate platforms (Mišík, 1993). In deeper areas of the Czorsztyn Unit, the Czorsztyn Formation was deposited until the Kimmeridgian. Its temporal development was characterized by compositional replacements of the main planktonic rock-forming components, including juvenile bivalves (*Bositra*) in the Bajocian-Callovian, globuligerinids in the Oxfordian, and *Saccocoma* in the Kimmeridgian. Note that these temporal replacements of dominating zooplankton are not local in nature because they were observed in the whole western Tethys (Martire, 1996). In shallower parts of the Czorsztyn Unit (Fig. 3), Bathonian-Kimmeridgian deposits were represented by non-nodular, micrite-rich or ammonite-rich limestones (Bohunice Formation) and crinoidal limestones with ammonite and brachiopod concentrations (Štepnica Formation). The Callovian-Lower Oxfordian deposits are mostly missing. They are preserved in dykes or as highly condensed firmgrounds and hardgrounds. The hiatus spanning the Callovian and Oxfordian is typical also of other pelagic carbonate platforms of the western Tethys (Bartolini and Cecca, 1999). Upper Kimmeridgian – Berriasian deposits are represented by the Dursztyn Formation with the shell-rich Rogoża (Kutek and Wierzbowski, 1986, Reháková and Wierzbowski, 2005) and Rogoźnik members (Kutek and Wierzbowski, 1979), and the micrite-rich Sobótka and Korowa members (Fig. 3). On the scale of the PKBB, brachiopods and bivalves reached their abundance peak in the Czorsztyn Unit.

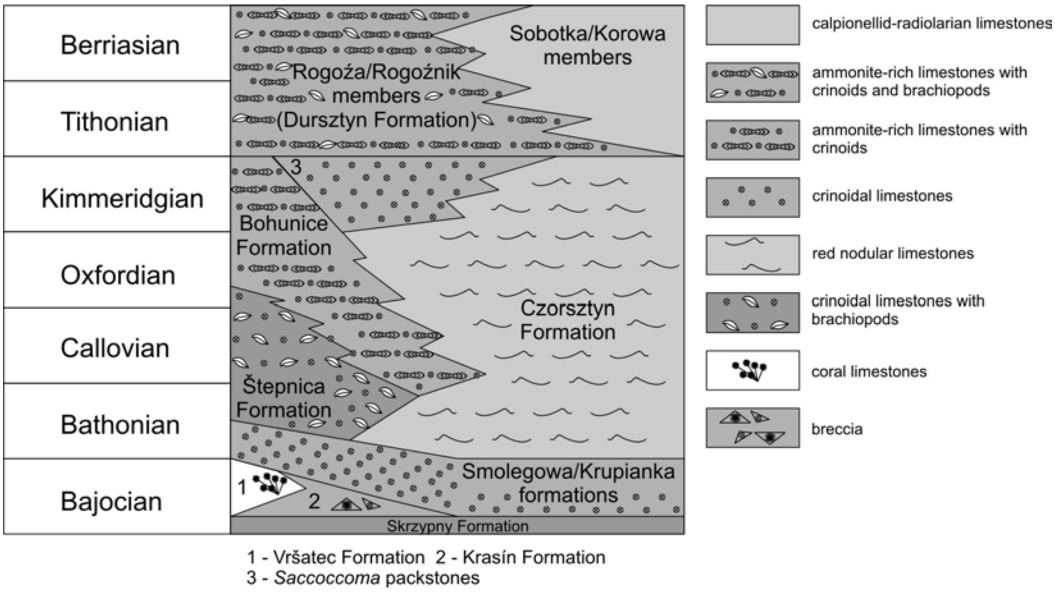


Figure 3 – Lithostratigraphic subdivision and spatial relationship of the Middle Jurassic-lowermost Cretaceous deposits of the Czorsztyn Unit (Pieniny Klippen Belt). Based on Aubrecht et al. (2002) and unpublished data.

Platform-basin transition. Transitional environments between the shallowest blocks of the Czorsztyn Unit and basinal environments of the Branisko and Pieniny units are preserved in the Pruské and Czertezik units. Crinoidal grainstones of the Smolegowa Formation or crinoidal-spiculitic limestones with cherts (Flaki Formation) have been deposited during the Bajocian (Wierzbowski et al., 2004). Red nodular limestones of the Niedzica Formation have been deposited during the uppermost Bajocian-Callovian. Deposition of radiolarites of the Czajakowa Formation took place during the Oxfordian. In deeper parts, deposition of radiolarites of the Czajakowa Formation started already in the uppermost Bajocian. Radiolarites were replaced by red nodular limestones during the Kimmeridgian and Early Tithonian. The Late Tithonian-Berriasian time interval was characterized by deposition of the micrite-rich Dursztyn Formation with calpionellids and radiolarians (Krobicki, 1993). Brachiopods were locally common in the Pruské (Krobicki, 1993) and Czertezik units (Wierzbowski et al., 2004), especially during the Tithonian-Berriasian. Bivalves were rare.

Basin. The Harcygrund Formation formed by *Bositra*-rich marls and marly limestones and the Podzamcze Formation consisting of grey bioturbated marlstones and limestones were deposited during the Early-early Late Bajocian in the Branisko and Pieniny units. Uppermost Bajocian-Oxfordian deposits are represented by radiolarites of the Sokolica Formation. During the Kimmeridgian, deposition of red nodular limestones took place in the Branisko Unit. The Tithonian/Berriasian deposits are represented by the plankton-rich Pieniny Formation with calpionellids and dinoflagellates.

Methods

The absolute abundance of brachiopod and bivalve individuals was estimated with the minimum number of individuals (MNI) approach (Gilinsky and Bennington, 1994). Untransformed relative abundances of brachiopods and bivalves from 53 samples were analyzed in exploratory and confirmatory multivariate analyses. 45 samples were based on field data and eight samples were compiled from literature data published by Siblík (1979) and Kochanová (1979). Brachiopods were determined to species level (A.T.) and bivalves to genus level (M.G.). Poor preservation of bivalves did not allow using species-level abundances although most of the bivalve taxa are probably represented by one species. Q-mode analyses were performed with these combined species/genus abundances because some brachiopod genera contain several species with distinct distribution. R-mode analyses were performed at genus level only. One-way ANOSIM tested the differences in community composition among (1) three habitats with distinct intensity of bottom currents (i.e., low-, moderate-, and high-energy habitats), and among (2) habitats with distinct substrate consistency (i.e., soft, mixed and hard substrates). Amalgamated sparitic beds were assigned to high-energy habitats, beds with complex internal stratification consisting of cm-scale alternation of background micritic and episodic shell-rich deposits to moderate-energy habitats, and homogeneous micritic beds to low-energy habitats. Densely-packed shell-rich deposits were assigned to hard substrates, wackestones/floatstones with crinoids, ammonites and brachiopods to mixed substrates and mudstones to soft substrates. Preservation of ammonites was studied in thin-sections in order to evaluate taphonomic bias against less durable aragonitic taxa. Proportions of fragmentation, bioerosion, dissolution relicts, Fe-coatings and Fe-infillings were scored on ammonites larger than 1 mm.

Sections

Macrobenthic assemblages with brachiopods and bivalves were sampled in 14 sections, which record various segments of the Middle and Upper Jurassic-lowermost Cretaceous succession of the Czorsztyn Unit. Brachiopods of Bajocian-Bathonian age were sampled in crinoidal and coral limestones, and from the sediment among clasts of the Krasín Breccia (Fig. 4). Coral limestones of the Vršatec Formation with branching and massive corals (Morycowa and Mišík, 2005) are overlying or laterally replacing breccia-rich sediments (Krasín Formation) in the Vršatec-Javorník 5 section (Fig. 4). Crinoidal wackestones and packstones of the Krupianka Formation with thin conglomeratic and breccia layers are exposed in the Mestečko (Fig. 4) and Babiná sections. Two samples are derived from red crinoidal-rich wackestones/floatstones of the Czorsztyn Formation.

Brachiopods of the Callovian-Oxfordian age were sampled in crinoidal, ammonite-rich and micritic limestones of the Štepnica and Bohunice formations (Fig. 5). Red nodular limestones of the Czorsztyn Formation of the Callovian-Oxfordian contain rare macrobenthos. The Štepnica Formation is represented by crinoidal wackestones and packstones with dispersed *Bositra* juveniles and brachiopods, which alternate with simple-event brachiopod and ammonite shell concentrations (rudstones). The Štepnica Formation overlies either red poorly nodular limestones in the Štepnická skala section or crinoidal limestones of the Smolegowa/Krupianka formations (Aubrecht et al., 2002).

The Bohunice Formation consists of alternations of ammonite-rich shell concentrations with wackestones and floatstones with *Bositra* (Upper Bathonian-Callovian), globuligerinids (Oxfordian), and *Saccocoma* (Kimmeridgian-Early Tithonian) (Mišík et al., 1994). The Bohunice Formation overlies either crinoidal limestones of the Smolegowa/Krupianka formations or crinoidal limestones of the Štepnica Formation. In the upper part, the Bohunice Formation gradually passes either into the Dursztyn Formation with ammonite shell concentrations (Babiná and Plaveč sections) or *Saccocoma* packstones (Štepnická skala section). Stromatactis-rich mud-mounds described by Aubrecht et al. (2002) are preserved in the upper part of the Štepnica Formation and the lower part of the Bohunice Formation. In the Vršatec-Javorník 4 section, the Bohunice Formation overlying Bajocian-Bathonian crinoidal limestones is reduced to three meters and encompasses the Oxfordian-Lower Kimmeridgian deposits only, implying a substantial stratigraphic gap at its lower boundary.

Brachiopods of the Kimmeridgian-Berriasian age were sampled in the Dursztyn Formation (Fig. 6). It overlies either the Bohunice Formation (Vršatec-Javorník 4, Plaveč), red *Saccocoma* packstones/grainstones (Štepnica - quarry B, Vieska-Bezdedov – Žiačik and Pod mokrou skalou sections) or red nodular limestones of the Czorsztyn Formation (Kyjov – Pusté Pole). The Dursztyn Formation is subdivided into the Rogoźa and Rogoźnik members with ammonite and crinoid concentrations, and the micrite-rich Sobotka and Korówa members with calpionellids and radiolarians. The Tithonian beds are commonly characterized by cm-scale alternations of ammonite floatstones and rudstones, and locally also by a 1 m-thick, amalgamated shell concentrations with ammonites.

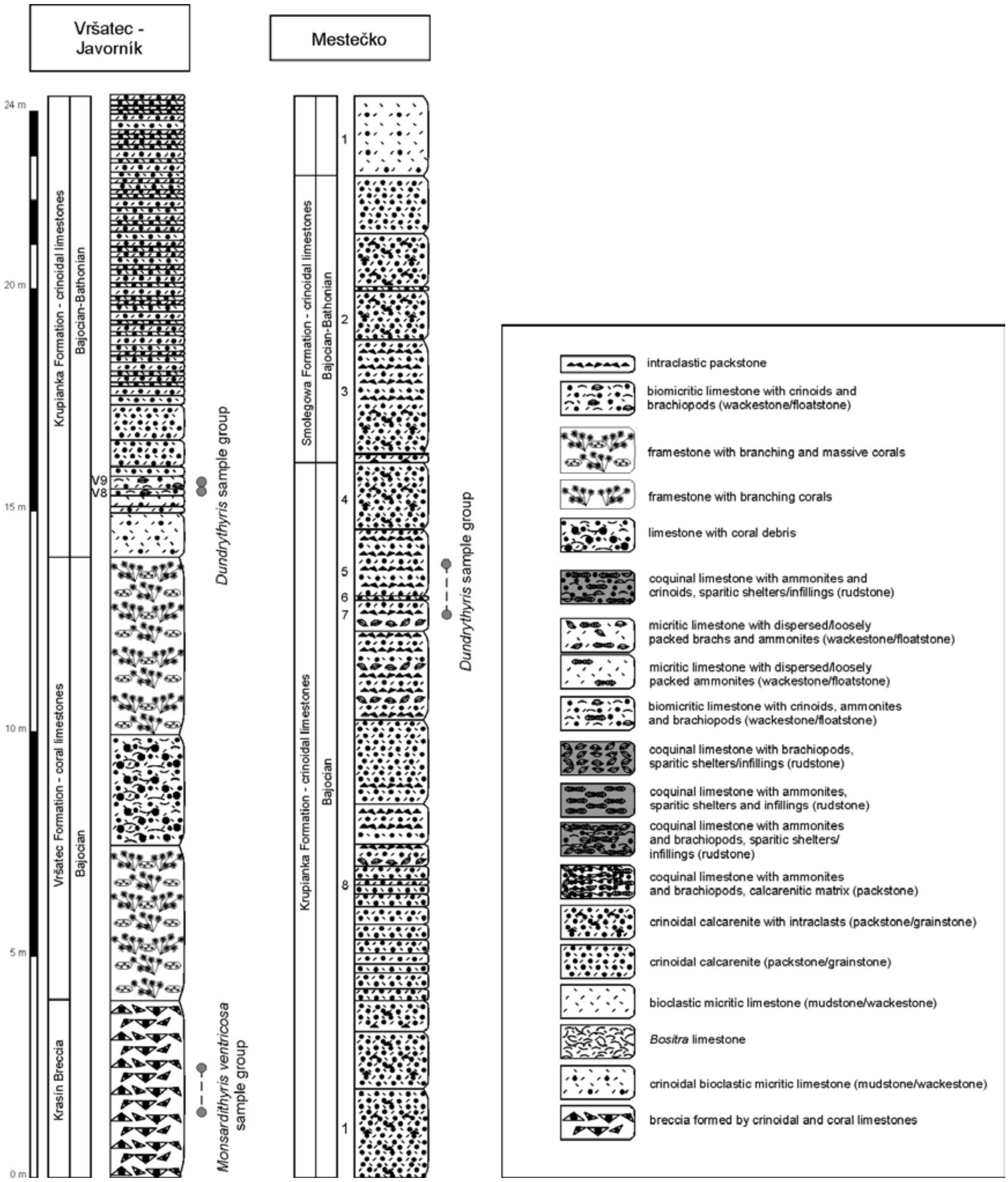


Figure 4 – Sedimentologic features and distribution of sample groups in two sections of the Bajocian-Bathonian.

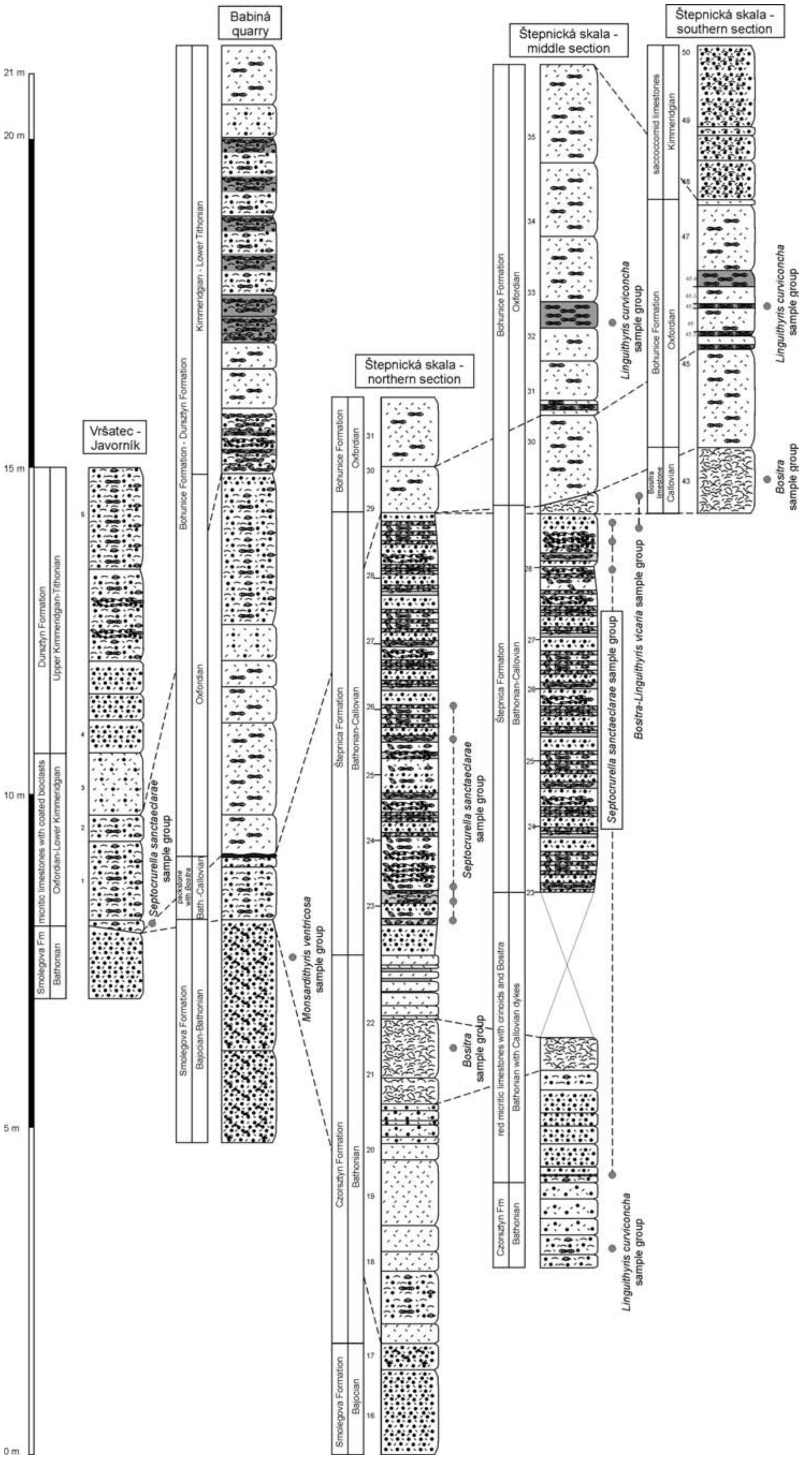


Figure 5 – Stratigraphic correlation, variation in facies development and distribution of sample groups in five sections of the Callovian-Oxfordian. Legend: see Figure 3.

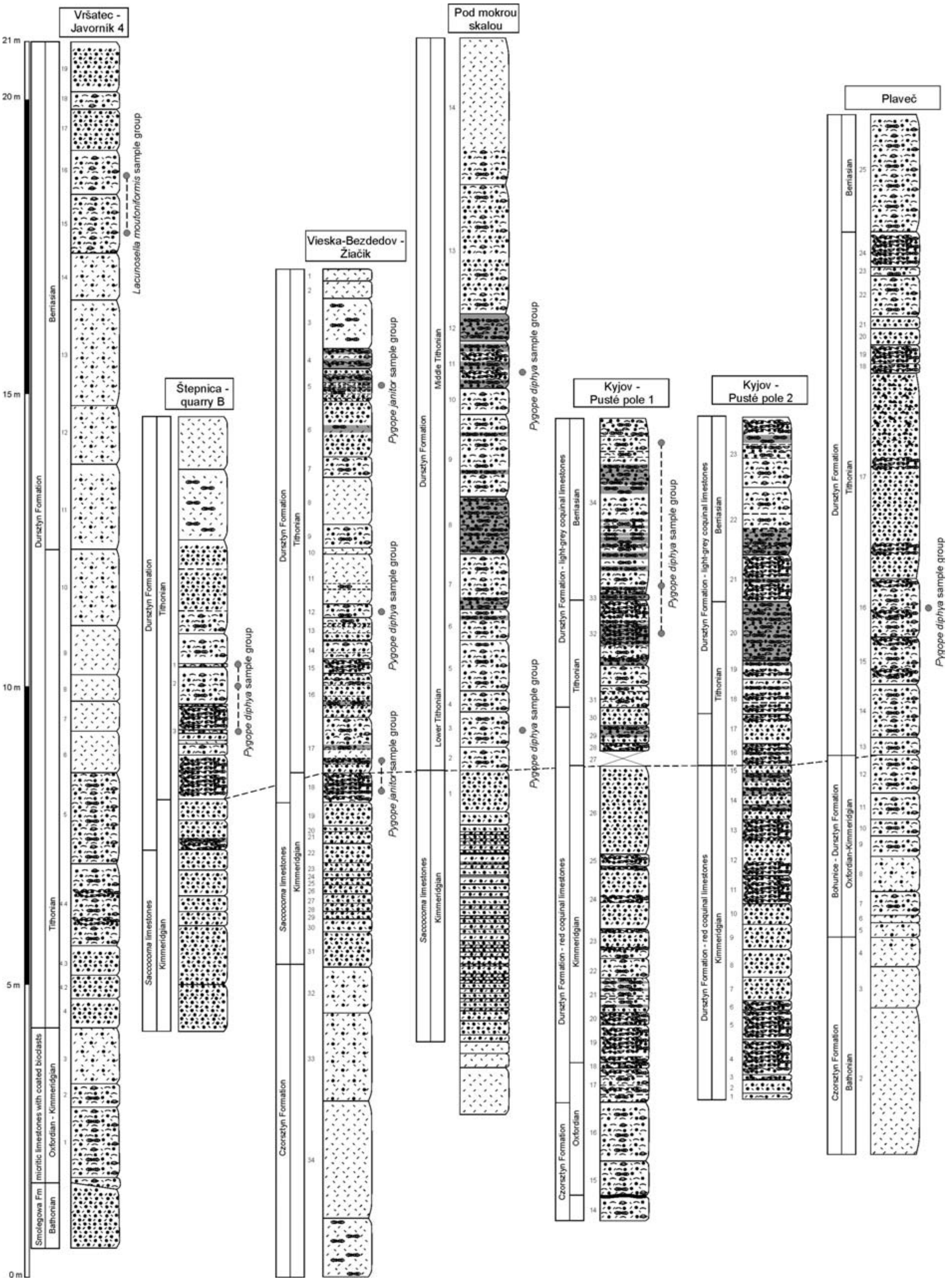


Figure 6 - Stratigraphic correlation, variation in facies development and distribution of sample groups in seven sections of the Kimmeridgian-Berriasian. Legend: see Figure 3.

Results

Discrimination of sample groups

A cluster analysis using the group-average linking method and Bray-Curtis similarity based on 53 samples and 3716 individuals was used for initial discrimination of 11 sample groups sharing similar abundances of brachiopods and bivalves (Fig. 7). Eight groups are dominated by brachiopods, two groups are dominated by epifaunal bivalves and one group is dominated both by brachiopods and bivalves (Figs. 8-10).

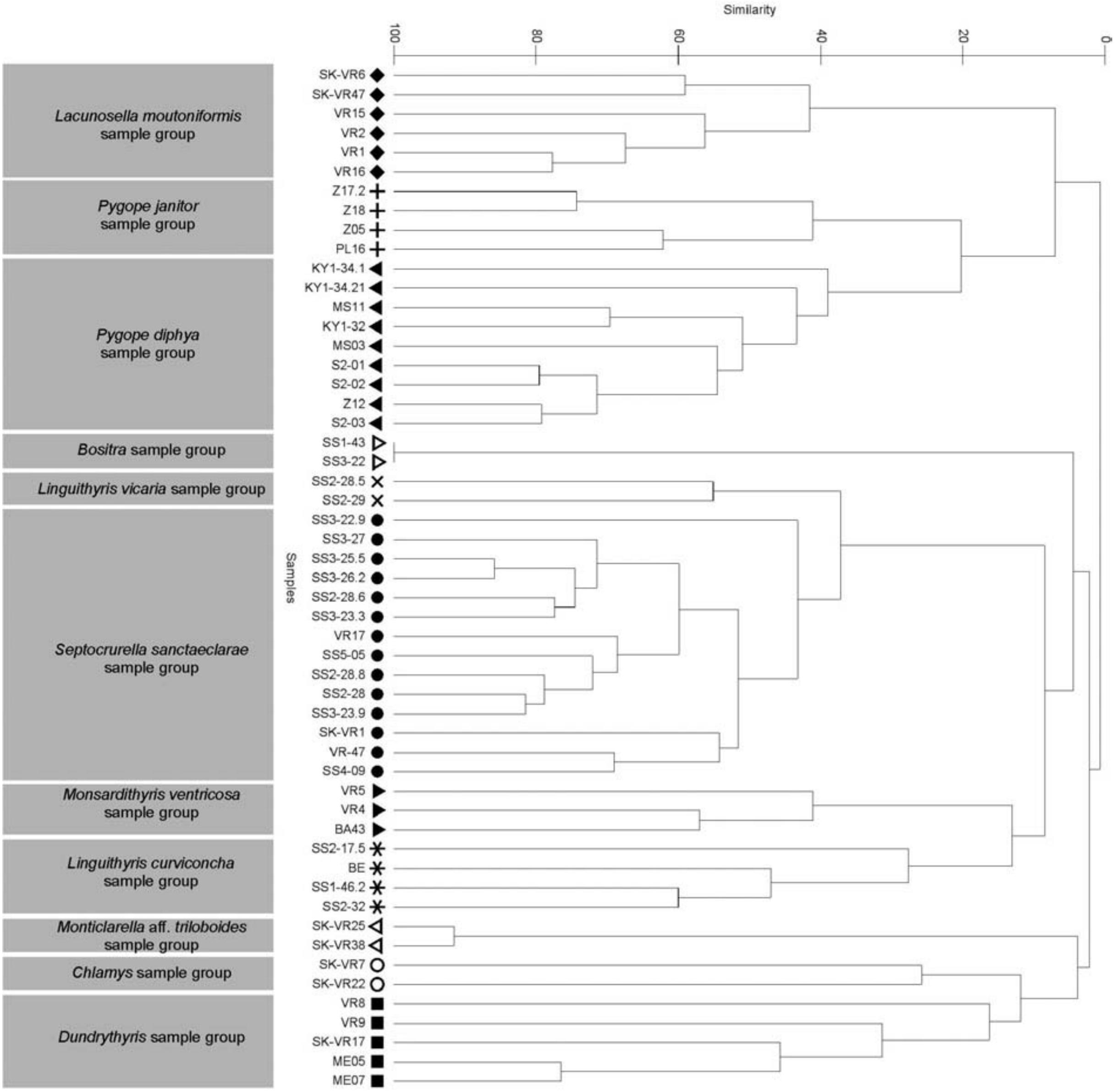


Figure 7 – Discrimination of 11 sample groups using Q-mode cluster analysis (Bray-Curtis similarities and the group average linking method) of 53 samples based on abundances of brachiopod species and bivalve genera.

(1) The *Dundrythyris* sample group is represented by five samples with 234 individuals. It is dominated by pedunculate brachiopods represented by the smooth terebratulid *Dundrythyris retrocarinata* (34%) and the multicostate rhynchonellids *Praelacunosella* aff. *dumortieri* (19%) and

Praelacunosella aff. *sublacunosa* (8%). The strongly biconvex terebratulid *Goniothyris hungarica* (7%) and the sulcate terebratulid *Linguithyris bifida* (6%) are less common. Bivalves are mainly represented by epibyssate filibranchs (7%, e.g., *Camptonectes, Chlamys, Oxytoma*). Free-lying (4%, e.g., *Propeamussium*) and cementing filibranchs (1%) are rare. This group is limited to red, well-sorted crinoidal-intraclastic limestones (Mestečko) and red, moderately sorted crinoidal wackestones/packstones (Vršatec) of the Bajocian.

(2) The *Monsardithyris ventricosa* sample group consists of three samples with 314 individuals. The uniplicate terebratulid *Monsardithyris ventricosa* (32%), the sulcate terebratulid *Antiptychina bivallata* (16%) and the multicostate rhynchonellid *Praelacunosella* aff. *sublacunosa* (15%) dominate. Other common pedunculate brachiopods are *Caucasella trigona* (8%), *Aulacothyris* sp. (7%), and *Linguithyris curviconcha* (6%). Bivalves are represented by the free-lying *Bositra buchi* (9%), epibyssate *Spondylopecten* sp. (1%), and rare endobyssate filibranchs (< 1%). The assemblages occur in shell-rich rudstones and packstones that form sediment infill among clasts of crinoidal and coral limestones (Krasín Formation) and in crinoidal limestones of the Smolegowa Formation (Babiná). They are probably of Bajocian age.

(3) The *Chlamys* sample group is represented by two samples formed by coral framestones and floatstones of the Vršatec Formation (Bajocian) with 116 individuals. The epibyssate bivalves *Chlamys* sp. (20%), *Spondylopecten* sp. (17%) and *Plagiostoma* sp. (13%) are abundant, followed by the pedunculate brachiopods *Praelacunosella* aff. *sublacunosa* (10%), *Zeilleria waltoni* (9%), and *Capillirhynchia* aff. *furcillata* (7%). The cementing filibranchs *Plicatula* sp. and *Placunopsis* sp. (5%) and the pseudolamellibranch *Lopha* sp. (3%) are less common. Free-lying filibranchs are rare (1%).

(4) The *Monticlarella* aff. *triloboides* sample group consists of two samples with 91 individuals from coral limestones of the Vršatec Formation (Bajocian). The group is strongly dominated by the pedunculate brachiopod *Monticlarella* aff. *triloboides* (87%) that occurs among coral branches. The epibyssate filibranchs *Chlamys* sp., *Spondylopecten* sp., and *Plagiostoma* sp. are common (11%), and the endobyssate filibranch *Modiolus* sp. is rare (2%).

(5) The *Linguithyris curviconcha* sample group consists of four samples with 2047 individuals. It is dominated by the sulcate terebratulid *Linguithyris curviconcha* (44%), followed by the endobyssate filibranch *Isoarca* sp. (6%), the pedunculate brachiopods *Karadagithyris eduardi* (10%), *Apringia* aff. *atla* (5%), and the shallow burrowing septibranch *Cuspidaria* sp. (5%). Epibyssate (*Plagiostoma, Camptonectes*) and free-lying filibranchs (*Bositra*) are common. Cementing filibranchs and shallow burrowing eulamellibranchs are rare (< 1%). Two samples are derived from red nodular limestones of the Czorsztyn Formation (Bathonian), and two samples are represented by ammonite-rich rudstones and packstones of the Bohunice Formation (Oxfordian).

(6) The *Septocrurella* sample group is represented by 14 samples with 1679 individuals. It is characterized by the dominance of the smooth or capillate, sulcate or rectimarginate pedunculate brachiopods *Septocrurella sanctaeclarae* (37%), *Monticlarella rollieri* (19%), *Karadagithyris decipiens* (18%), and *Linguithyris vicaria* (13%). The brachiopods *Linguithyris curviconcha* (5%) and *Aulacothyris* sp. (3%), and the epifaunal filibranchs *Plagiostoma* sp., *Bositra buchi*, and *Spondylopecten* sp. (3%) are less common. Other bivalve guilds, represented by cementing filibranchs, endobyssate filibranchs, shallow burrowing eulamellibranchs, and septibranchs, are rare (< 1%). This group occurs in multiple-event crinoidal packstones and ammonite-brachiopod rudstones of the Štepnica Formation (Callovian) and in Oxfordian dykes formed by red floatstones/packstones.

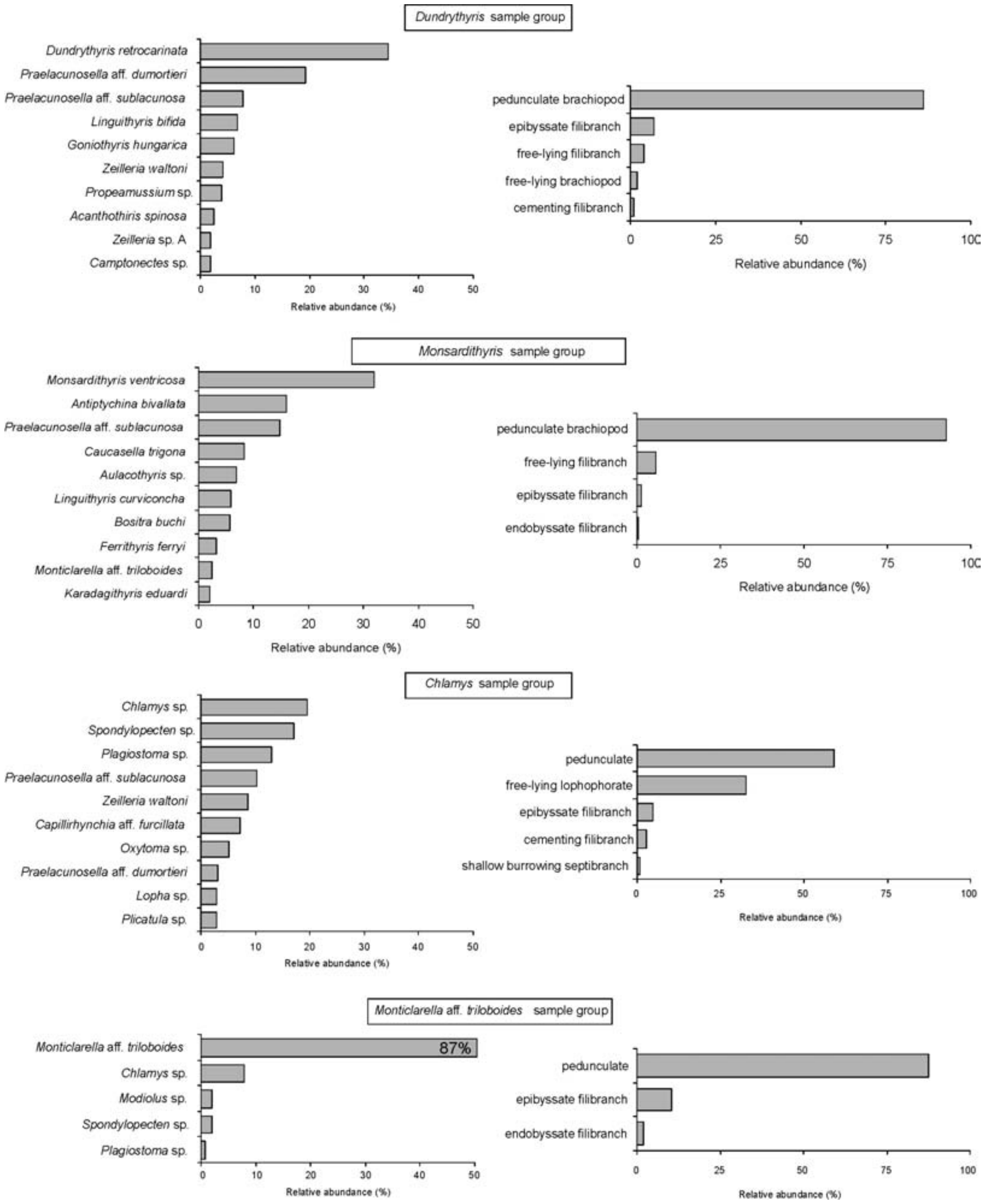


Figure 8 – Relative abundances of taxa and guild composition of four sample groups typical of the Bajocian-Bathonian deposits of the Pieniny Klippen Belt.

(7) The *Bositra*-*Linguithyris vicaria* sample group consists of two samples and 163 individuals. It is dominated by the free-lying filibranch *Bositra buchi* (34%) and the sulcate terebratulid *Linguithyris vicaria* (30%). The pedunculate brachiopods *Karadagithyris decipiens* (15%), *Monticlarella rollieri* (8%), *Septocrurella sanctaeclarae* (6%), and *Linguithyris curviconcha* (5%) are less common. This group is limited to crinoidal and coquinal floatstones and rudstones in the upper parts of the Štepnica Formation (Callovian). One sample at the boundary between the Štepnica and Bohunice formations laterally passes into monospecific coquinal rudstone with *Bositra buchi* (*Bositra* sample group).

(8) The *Bositra* sample group is represented by two samples with a monospecific assemblage of the free-lying bivalve *Bositra buchi*. One sample at the boundary between the Štepnica and Bohunice formations is represented by a laterally restricted rudstone lense with flat base and convex upper bedding plane. It changes in thickness from 70 cm to zero within several meters. Another sample is similarly derived from a lensoid rudstone bed, which is present in the upper parts of the Czorsztyn Formation. Both beds may represent dyke infillings (Callovian).

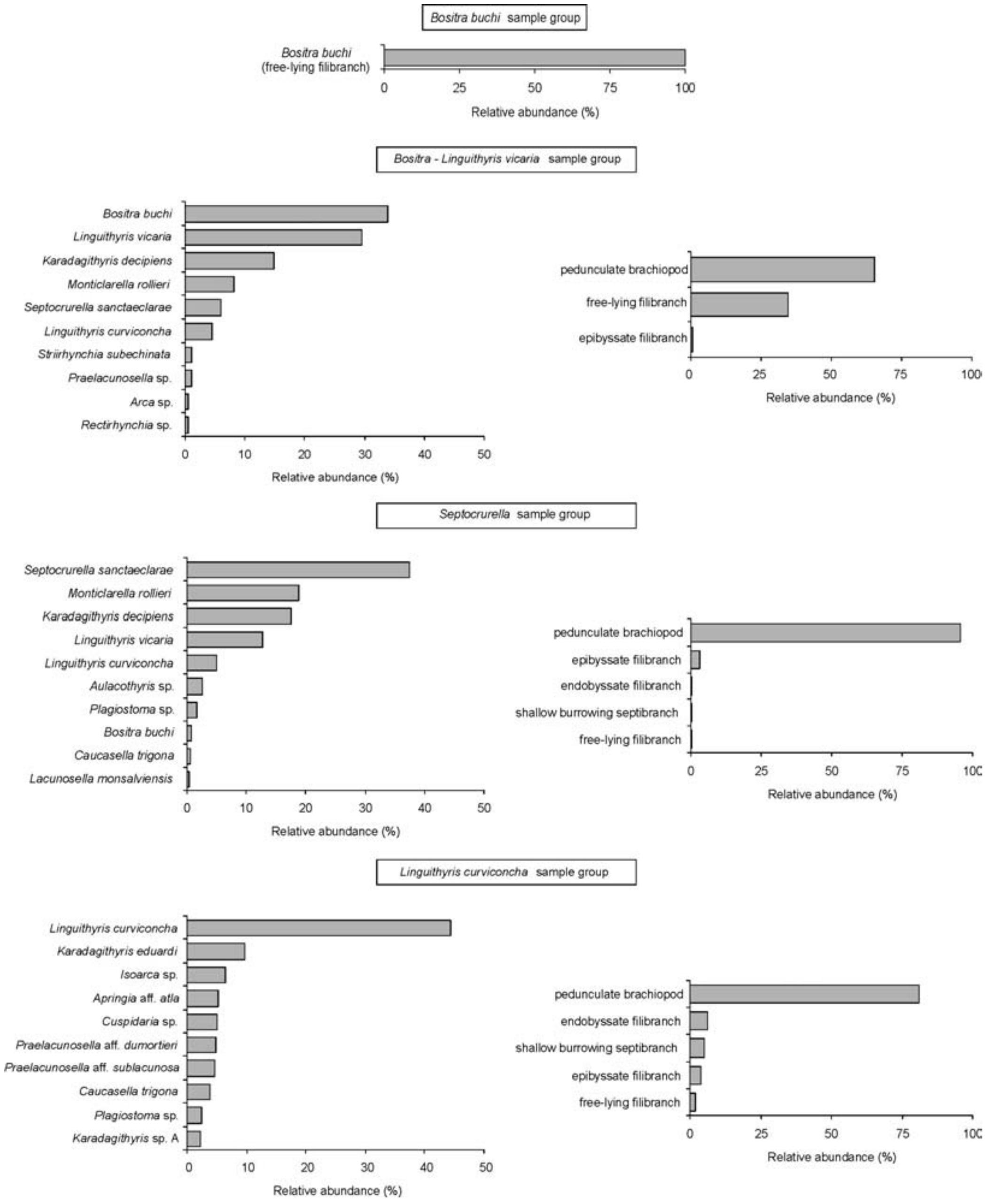


Figure 9– Relative abundances of taxa and guild composition of four sample groups typical of the Callovian-Oxfordian deposits of the Pieniny Klippen Belt.

(9) The *Pygope janitor* sample group is represented by four samples with 258 individuals. It is strongly dominated by the bilobate terebratulid *Pygope janitor* (52%), followed by the rhynchonellid *Monticlarella capillata* (14%) and the terebratulid *Nucleata planulata* (13%). *Monticlarella agassizi* (3%) and *Karadagithyris bilimeki* (2%) are less common. Bivalves are represented mainly by epibyssate filibranchs (11%) such as *Pseudolimea* sp., *Plagiostoma* sp., and *Spondylopecten* sp. Cementing, endobyssate and free-lying filibranchs and shallow burrowing

eulamellibranchs are rare (1%). This group occurs in crinoidal-bioclastic grainstones/rudstones and floatstones with *Saccocoma* and juvenile ammonites (Dursztyn Formation). They are of the Late Kimmeridgian-Tithonian age.

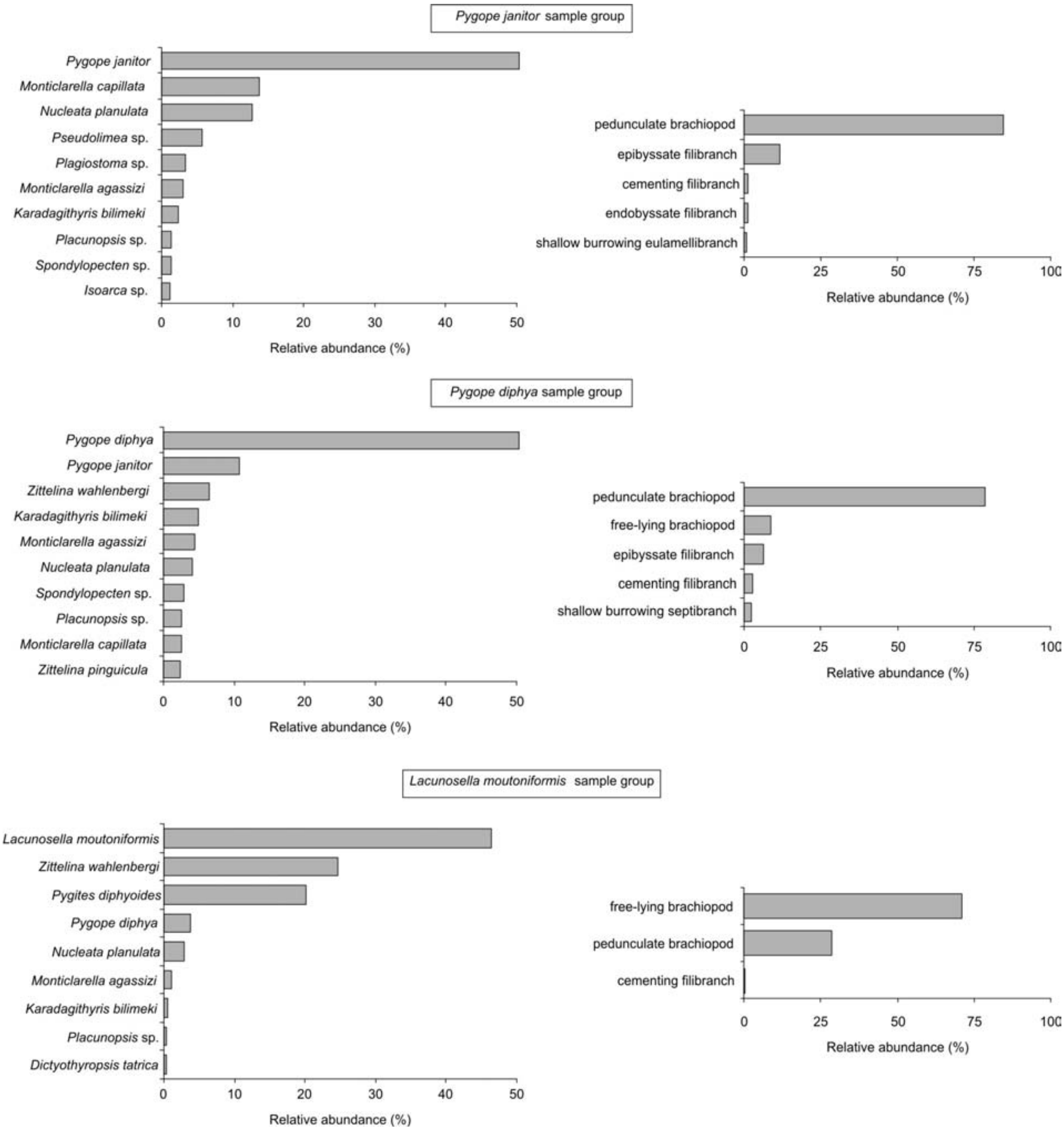


Figure 10 – Relative abundances of taxa and guild composition of three sample groups typical of the Kimmeridgian-Berriasian deposits of the Pieniny Klippen Belt.

(10) The *Pygope diphya* sample group consists of nine samples with 326 individuals and is dominated by the bilobate terebratulid *Pygope diphya* (51%). The pedunculate brachiopods *Pygope janitor* (11%), *Karadagithyris bilimeki* (5%), *Monticlarella agassizi* (5%), *Nucleata planulata* (4%), and *Monticlarella capillata* (3%) are less common. *Zittelina wahlenbergi* (6%) and *Zittelina pinguicula* (2%) probably represent a free-lying guild of brachiopods. Epibyssate filibranchs with *Spondylopecten* sp. (3%) and cementing filibranchs with *Placunopsis* sp. (3%) are common. Shallow burrowing septibranchs (2%), endobyssate (1%) and free-lying filibranchs (1%), and shallow burrowing eulamellibranchs are rare (< 1%). This group occurs mainly in ammonite rudstones,

ammonite floatstones with juvenile ammonites and *Saccocoma* packstones of the Dursztyn Formation (Tithonian-Berriasian).

(11) The *Lacunosella moutoniformis* sample group is represented by six samples with 241 individuals. It is characterized by the dominance of free-lying (*Lacunosella moutoniformis* [46%] and *Zittelina wahlenbergi* [24%]) and pedunculate brachiopods (*Pygites diphyoides* [20%]). Other pedunculate brachiopods (*Pygope diphya, Nucleata planulata, Monticlarella agassizi*, and *Karadagithyris bilimeki*) are less common or rare. Bivalves are represented by rare cementing filibranchs (*Placunopsis* sp.). This group occurs in crinoidal wackestones and packstones of the Dursztyn Formation (Berriasian).

One-way ANOSIM-temporal differences	R	p-value	Number of permutations	Number of permuted R≥observed R
Taxonomic composition	0.746	<0.0001	10000	0
Global test				
Kimmeridgian-Tithonian vs. Bajocian-Bathonian	0.724	<0.0001	10000	0
Kimmeridgian-Tithonian vs. Callovian-Oxfordian	0.859	<0.0001	10000	0
Kimmeridgian-Tithonian vs. Berriasian	0.708	0.0001	10000	1
Bajocian-Bathonian vs. Callovian-Oxfordian	0.639	<0.0001	10000	0
Bajocian-Bathonian vs. Berriasian	0.729	<0.0001	10000	0
Callovian/Oxfordian vs. Berriasian	0.844	<0.0001	10000	0
Guild composition				
Global test	0.254	<0.0001	10000	0
Kimmeridgian-Tithonian vs. Bajocian-Bathonian	-0.029	0.67	10000	6730
Kimmeridgian-Tithonian vs. Callovian-Oxfordian	0.011	0.37	10000	3760
Kimmeridgian-Tithonian vs. Berriasian	0.969	<0.0001	10000	0
Bajocian-Bathonian vs. Callovian-Oxfordian	0.004	0.36	10000	3644
Bajocian-Bathonian vs. Berriasian	0.764	<0.0001	10000	0
Callovian/Oxfordian vs. Berriasian	0.691	<0.0001	10000	0

Table 1 - Results of analysis of similarities (ANOSIM) testing differences in taxonomic and guild abundances among four time intervals.

Temporal differences in community composition

There are significant differences in taxonomic composition ($R = 0.75$, $p < 0.0001$, Tab. 1) among four time segments (i.e., Bajocian-Bathonian, Callovian-Oxfordian, Kimmeridgian-Tithonian, and Berriasian). This temporal effect can be expected because the whole time interval spans about 40-50 Ma. Therefore, community analyses were performed separately for each time interval, with the Berriasian samples analyzed together with the Upper Jurassic samples because of low sample number. The differences in guild composition among four time segments are much lower ($R = 0.25$, $p < 0.0001$) and the main difference is between the Berriasian on one hand and the other three time segments on the other hand (Tab. 1). The Berriasian communities were dominated by free-lying brachiopods and the Middle-Late Jurassic communities by pedunculate brachiopods. Interestingly, the guild structure of the Middle and Late Jurassic communities was rather constant, with pedunculate brachiopods (80-87%) and epibyssate filibranch bivalves (2.5-13%) being most abundant. Free-lying filibranchs represented by *Bositra* were common during the Callovian-Oxfordian (14%). Cementing filibranchs (0.2-2%), endobyssate filibranchs (0.3-1.5%), shallow burrowing septibranchs (0-1.2%) and shallow burrowing eulamellibranchs (0-0.4%) were rare.

Co-occurrence patterns of brachiopods and bivalves

Bajocian-Bathonian. R-mode NMDS based on genus abundances shows a rather high overlap in brachiopod and bivalve abundances in two dimensions (Fig. 11A). However, the overlap is smaller in three dimensions. The differences between brachiopod and bivalve abundances are low but significant using ANOSIM (R = 0.271, $p < 0.0001$, Tab. 2). Pedunculate brachiopods show similar abundance patterns mainly with free-lying (BC = 28) and epibyssate filibranchs (BC = 26) in R-mode NMDS based on guild abundances (Fig. 11B). Bray-Curtis similarity between pedunculate brachiopods and other bivalve guilds is below 15.

R-mode based ANOSIM - brachiopod vs. bivalve genera	R	p-value	Number of permutations	Number of permuted R≥observed R
Bajocian-Bathonian	0.271	<0.0001	10000	0
Callovian-Oxfordian	0.312	0.0001	10000	1
Kimmeridgian-Berriasian	0.209	0.016	10000	156

Table 2 – Results of analysis of similarities (ANOSIM) testing differences in abundance patterns between brachiopods and bivalves.

Callovian-Oxfordian. R-mode NMDS based on genus abundances indicates a poor segregation between brachiopods and bivalves because some bivalves occur more with brachiopods than with other bivalves (Fig. 11C). The differences between brachiopod and bivalve abundances are significant although relatively low (ANOSIM, R = 0.312, p = 0.001, Tab. 2). In R-mode NMDS based on guild abundances (Fig. 11D), pedunculate brachiopods possess a higher similarity in abundance patterns with epibyssate filibranchs (BC = 22) than with other bivalve guilds (BC is lower than 15).

Kimmeridgian-Berriasian. There are significant differences between brachiopod and bivalve abundances (ANOSIM, R = 0.209, p = 0.016, Tab. 2). This difference is also visible in the segregation of brachiopods and bivalves in R-mode NMDS based on genus abundances (Fig. 11E). In R-mode NMDS based on guild abundances (Fig. 11F), pedunculate brachiopods show similar abundance patterns with cementing (BC = 48), epibyssate (BC = 47) and endobyssate filibranch bivalves (BC = 33). They have lower similarities with shallow burrowing septibranchs (BC = 8%), free-lying filibranchs (BC = 11) and shallow burrowing eulamellibranchs (BC = 15).

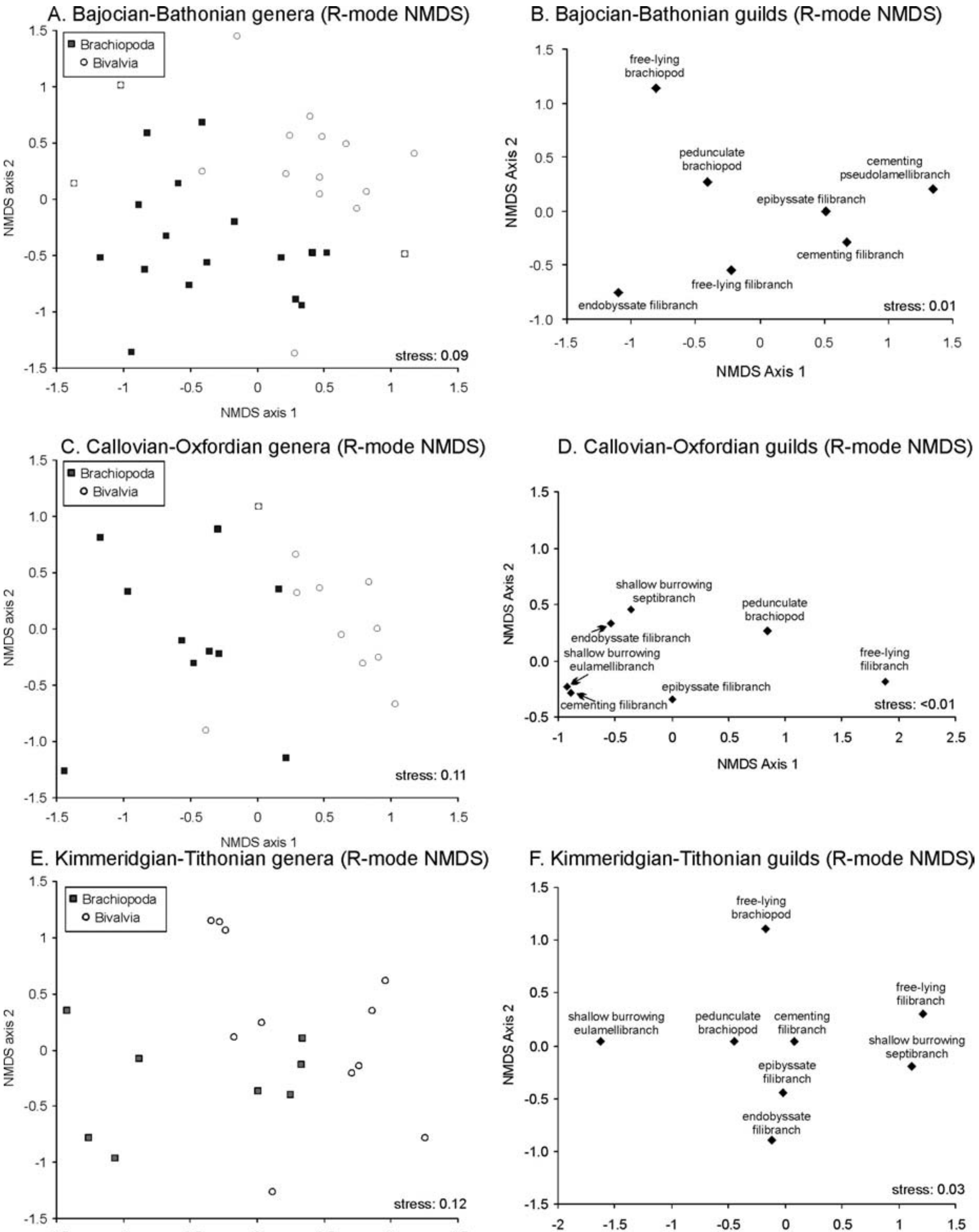


Figure 11 – Co-occurrence patterns between brachiopod and bivalve genera and between brachiopod and bivalve guilds. A. R-mode non-metric multidimensional scaling (NMDS) based on abundances of Bajocian-Bathonian taxa. B. R-mode NMDS based on abundances of Bajocian-Bathonian guilds. C. R-mode NMDS based on abundances of Callovian-Oxfordian taxa. D. R-mode NMDS based on abundances of Callovian-Oxfordian guilds. E. R-mode NMDS based on abundances of Kimmeridgian-Berriasian taxa. F. R-mode NMDS based on abundances of Kimmeridgian-Berriasian guilds.

Habitat differences reflected by community composition

Bajocian-Bathonian

Differences in bottom currents. ANOSIM shows that differences in community composition between habitats differing in the intensity of bottom currents are significant (R = 0.69, p = 0.002, Tab. 3). This difference is visualized in Q-mode NMDS in Figure 12A. Low-energy habitats were dominated by the sulcate terebratulid *Linguithyris curviconcha* and the multicostate rhynchonellid *Praelacunosella* aff. *sublacunosa* (Fig. 13A). Habitats with moderate intensity of bottom currents were dominated by the terebratulid *Dundrythyris retrocarinata* and the multicostate rhynchonellid *Praelacunosella* aff. *dumortieri* (Fig. 13A). High-energy habitats were dominated by the terebratulids *Monsardithyris ventricosa* and *Antiptychina bivallata*. There is a high overlap in Q-mode NMDS (Fig. 12B) and poor differences in guild abundance between the habitats with different intensity of bottom currents (R = 0.388, p = 0.054, Tab. 3). Pedunculate brachiopods heavily dominated in all habitats (Fig. 14A). Bivalve guilds attained minor abundance (1-2%) in low- and moderate-energy habitats. Free-lying filibranchs (*Bositra buchi*) were relatively abundant (10%) in high-energy habitats. Coral deposits were evaluated separately because they could not be assigned to the three-fold subdivision of the habitats. Epibyssate (83%) and cementing filibranchs (9%) were abundant in coral-rich framestones and floatstones.

Substrate differences. ANOSIM indicates that three habitats with different substrate types were inhabited by communities that significantly differ in their composition (R = 0.38, p = 0.02, Tab. 3). In terms of guild abundance, there are poor differences in community composition among the habitats with four distinct substrate types (R = 0.39, p = 0.054, Tab. 3). Soft and mixed substrates were dominated by the terebratulid *Dundrythyris retrocarinata* and the multicostate rhynchonellids *Praelacunosella* aff. *dumortieri* and *Praelacunosella* aff. *sublacunosa*.

One-way ANOSIM-Bajocian-Bathonian	R	p-value	Number of permutations	Number of permuted R≥observed R
Taxonomic composition				
Substrate differences				
Global test	0.378	0.02	6435	130
mixed-bottom, hard-bottom	0.542	0.006	495	495
hard-bottom, soft-bottom	-0.286	(0.88)	9	9
mixed-bottom, soft-bottom	0.417	(0.2)	5	5
Bottom current differences				
Global test	0.685	0.002	1260	2
High-energy vs. moderate-energy habitats	0.857	(0.067)	15	1
High-energy vs. low-energy habitats	0.167	(0.3)	10	3
Low-energy vs. moderate-energy habitats	0.778	(0.029)	35	1
Guild composition				
Substrate differences				
Global test	0.064	0.32	6435	2065
Bottom current differences				
Global test	0.388	0.054	1260	68

Table 3 - Results of analysis of similarities (ANOSIM) of Bajocian-Bathonian samples showing differences in taxonomic and guild composition among habitats differing in the intensity of bottom currents and substrate types.

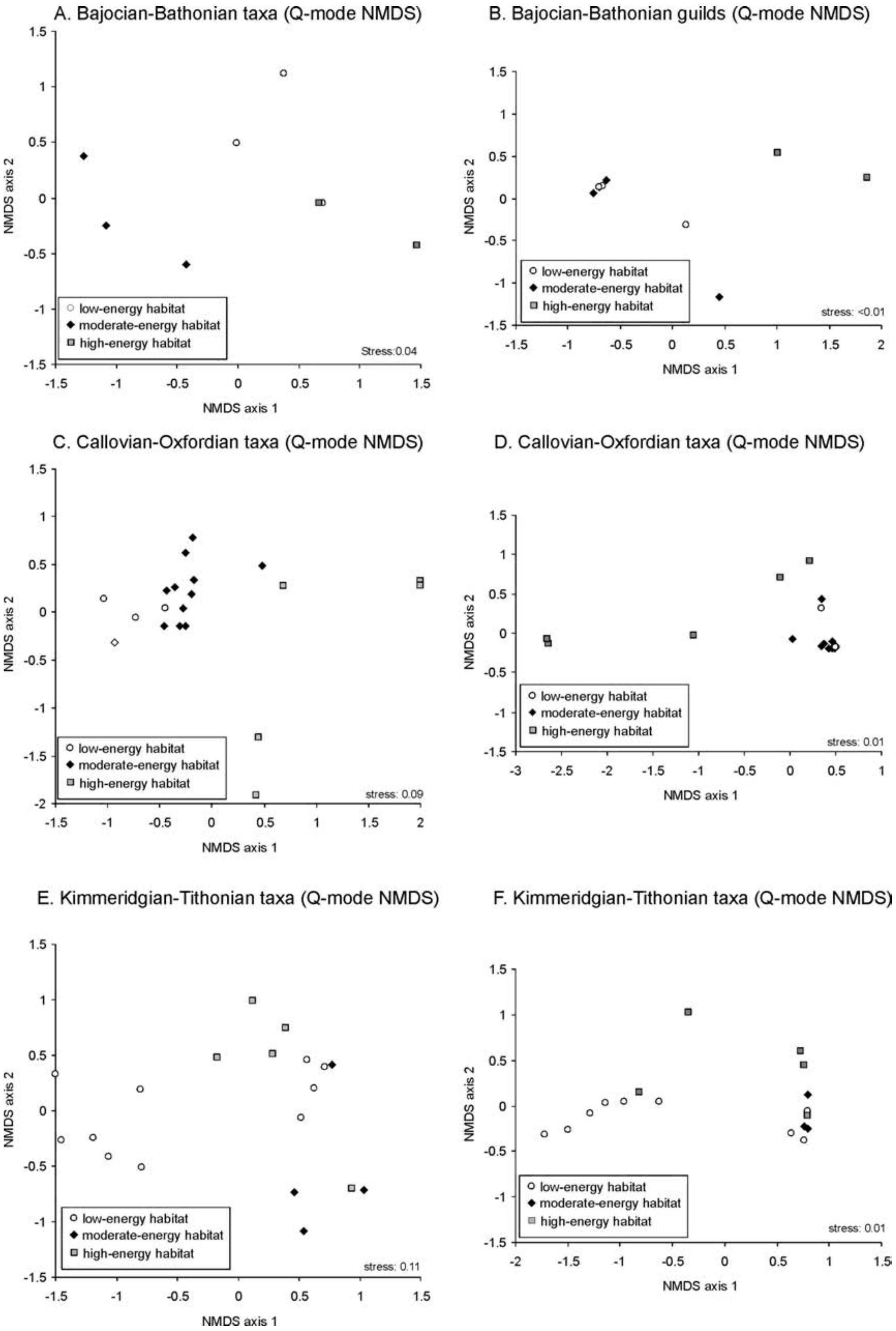


Figure 12 – Compositional differences among habitats differing in the intensity of bottom currents are visualized by Q-mode non-metric multidimensional scaling (NMDS) based on taxonomic and guild abundances of brachiopods and bivalves. These plots complement ANOSIM tests that are also based on rank order, Bray-Curtis dissimilarity matrices. A. Q-mode NMDS based on abundances of Bajocian-Bathonian taxa. B. Q-mode NMDS based on abundances of Bajocian-Bathonian guilds. C. Q-mode NMDS based on abundances of Callovian-Oxfordian taxa. D. Q-mode NMDS based on abundances of Callovian-Oxfordian guilds. E. Q-mode NMDS based on abundances of Kimmeridgian-Berriasian taxa. F. Q-mode NMDS based on abundances of Kimmeridgian-Berriasian guilds.

Hard substrates were inhabited mainly by *Monsardithyris ventricosa, Antiptychina bivallata* and *Monticlarella* aff. *triloboides*. Epibyssate filibranchs were common on mixed (9%) and hard substrates (6%) and rare on hard substrates (1%). Free-lying filibranchs were comparatively common on all three substrates (3-4%). Coral substrates were dominated by the epibyssate bivalves (83%, e.g., *Spondylopecten* sp., *Plagiostoma* sp. and *Chlamys* sp.), cementing filibranchs (9%), and cementing pseudolamellibranchs (6%).

Callovian-Oxfordian

Differences in bottom currents. ANOSIM and Q-mode NMDS (Fig. 12C) show that there are significant differences in taxonomic composition among habitats differing in the intensity of bottom currents (R = 0.58, p = 0.0003, Tab. 4). Pairwise comparisons indicate that the communities from high-energy habitats strongly differ from the communities from moderate-energy habitats (R = 0.82, p = 0.0002) and low-energy habitats (R = 0.49, p = 0.036). The rhynchonellid *Septocrurella sanctaeclarae* accompanied by the rhynchonellid *Monticlarella rollieri* and the terebratulid *Karadagithyris decipiens* were the most abundant brachiopods in habitats characterized by low and moderate intensity of bottom currents. *Linguithyris vicaria* reached its abundance peak in habitats with moderate intensity of bottom currents (Fig. 13B). High-energy habitats were dominated by the epibyssate bivalve *Bositra buchi* and the terebratulid *Linguithyris curviconcha* (Fig. 13B). In contrast to the Bajocian-Bathonian time interval, there are significant differences in guild abundance between habitats differing in the intensity of bottom currents (R = 0.55, p = 0.001, Tab. 4). This difference is caused by the differential abundance of pedunculate brachiopods and free-lying bivalves between high-energy habitats on one hand and low- and moderate-energy habitats on the other hand (Fig. 12D). Pedunculate brachiopods decreased and bivalve guilds increased in abundance towards high-energy habitats. Bivalves were less common in low-energy (5%) and moderate-energy habitats (5%) but dominated in high-energy habitats (54%).

Substrate differences. ANOSIM demonstrates that there are insignificant differences in taxonomic composition (R = 0.11, p = 0.11, Tab. 4) and guild abundance (R = 0.11, p = 0.1, Tab. 4) among habitats with different substrate types. Pedunculate brachiopods were most abundant on soft-bottom (93%) and mixed-bottom substrates (97%) and less abundant on hard substrates (61%). Free-lying filibranchs were abundant on hard substrates (32%) but rare on soft and mixed substrates (0-1%). Epibyssate filibranchs were common on soft substrates (6%) and rare on mixed (2%) and hard substrates (2%). Shallow burrowing bivalves were rare in all three habitats (< 1%).

Kimmeridgian-Berriasian

Differences in bottom currents. The differences in community composition among habitats differing in the intensity of bottom currents are very low with ANOSIM (R = 0.17, p = 0.057, Tab. 5) and in Q-mode NMDS (Fig. 12E). The bilobate terebratulid *Pygope diphya* shows a bimodal abundance distribution because it was dominant both in low-energy and high-energy habitats. The rhynchonellid *Lacunosella moutoniformis* and the terebratulid *Pygites diphyoides* were abundant in low-energy habitats (Fig. 13C). Moderate-energy habitats were dominated by *Pygope janitor* and *Nucleata planulata*. In terms of guild abundances, there are no significant differences among habitats differing in the intensity of bottom currents with ANOSIM (R = 0.09, p = 0.16, Tab. 5) and in Q-mode NMDS (Fig. 12F). Pedunculate brachiopods reached their abundance peak in habitats with moderate intensity of bottom currents, and free-lying brachiopods in habitats with low intensity of bottom currents. Bivalve guilds were rare in low-energy habitats (1.5%), more common in the habitats with moderate-energy habitats (10%) and most abundant (mainly epibyssate and cementing filibranchs and shallow burrowing septibranchs) in high-energy habitats (24%).

One-way ANOSIM-Callovian-Oxfordian	R	p-value	Number of permutations	Number of permuted R≥observed R
Taxonomic composition				
Substrate differences				
Global test	0.114	0.11	10000	1103
Bottom current differences				
Global test	0.576	0.0003	10000	3
Low-energy vs. moderate-energy habitats	0.102	0.32	455	144
High-energy vs. low-energy habitats	0.492	(0.036)	56	2
High-energy vs. moderate-energy habitats	0.825	0.00016	6188	1
Guild composition				
Substrate differences				
Global test	0.117	0.108	10000	1077
Bottom current differences				
Global test	0.547	0.0014	10000	14
Low-energy vs. moderate-energy habitats	-0.019	0.48	455	219
High-energy vs. low-energy habitats	0.241	(0.125)	56	7
High-energy vs. moderate-energy habitats	0.855	0.00016	6188	1

Table 4 - Results of analysis of similarities (ANOSIM) of Callovian-Oxfordian samples showing differences in taxonomic and guild abundances among habitats differing in the intensity of bottom currents and substrate types.

One-way ANOSIM-Kimmeridgian-Berriasian	R	p-value	Number of permutations	Number of permuted R≥observed R
Taxonomic composition				
Substrate differences				
Global test	0.007	0.407	10000	4067
Bottom current differences				
Global test	0.173	0.057	10000	571
High-energy vs. low-energy habitats	0.086	0.17	4368	734
High-energy vs. moderate-energy habitats	0.487	(0.11)	56	6
Low-energy vs. moderate-energy habitats	0.243	0.039	364	14
Guild composition				
Substrate differences				
Global test	0.039	0.269	10000	2690
Bottom current differences				
Global test	0.012	0.36	10000	3629
High-energy vs. low-energy habitats	0.056	0.22	4368	957
High-energy vs. moderate-energy habitats	0.108	(0.2)	56	11
Low-energy vs. moderate-energy habitats	-0.057	0.58	364	210

Table 5 - Results of analysis of similarities (ANOSIM) of Kimmeridgian-Berriasian samples showing differences in taxonomic and guild abundances among habitats differing in the intensity of bottom currents and substrate types.

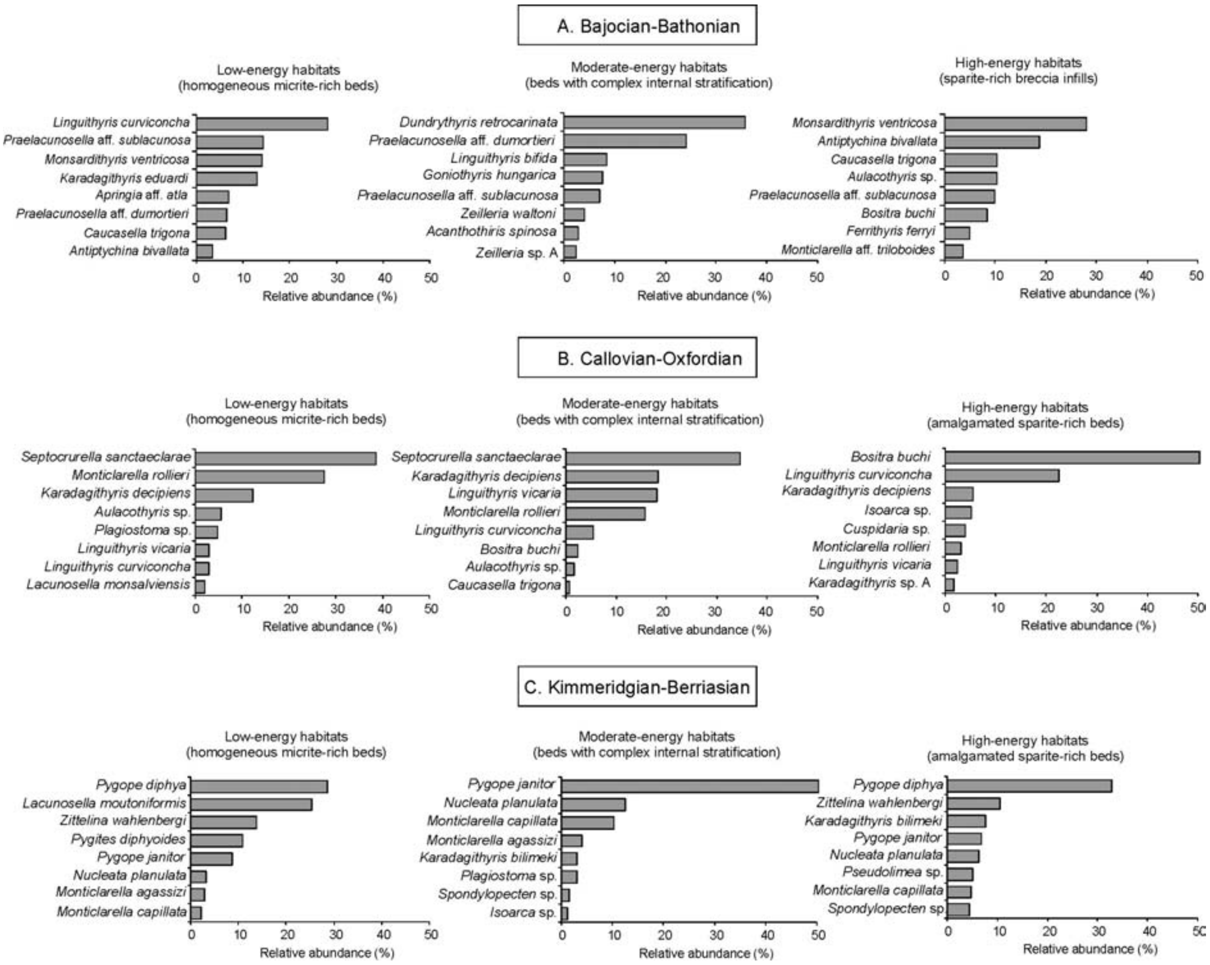


Figure 13 – Relative abundances of taxa in three habitats differing in the intensity of bottom currents during three time intervals. A. Bajocian-Bathonian. B. Callovian-Oxfordian. C. Kimmeridgian-Berriasian.

Substrate differences. ANOSIM shows that there are minimal and insignificant differences in taxonomic composition (R = 0.07, p = 0.4, Tab. 5) and guild abundance (R = 0.039, p = 0.27) among habitats differing in substrate types. Pedunculate brachiopods dominated on hard (65%), mixed (61%) and soft substrates (88%). Epibyssate filibranchs were common on hard (14%) and soft substrates (6%), and rare on mixed substrates (1%). Shallow burrowing bivalves were rare on all three substrates, although *Cuspidaria* occurred mainly on hard substrates (3%).

Taphonomic bias against less durable aragonitic taxa

Aragonite dissolution in the taphonomic active zone (TAZ) is evidenced by presence of ammonite shell walls filled by interstitial sediment (Fig. 15E), bored and encrusted molds and isolated Fe-rich coatings (biofilms) that remained after dissolution of their aragonitic substrate. In contrast, calcitic taxa such as brachiopods do not show any signs of dissolution. Radiaxial fibrous calcite cements overlain by internal sediment (Fig. 15C) indicate that aragonite dissolution was coupled with rapid calcite cementation in the TAZ (cf., Palmer and Wilson, 2004). Importantly, dissolution as the most probable destruction mechanism that accounts for differential durability of aragonitic vs. calcitic taxa left its pathway in the sediments. Fragments of ammonites and bivalves were commonly coated with Fe-biofilms when exposed on the sea-floor (Fig. 16). Aragonite dissolution took place subsequently during very shallow burial in the TAZ. As a consequence, proportions of floating Fe-rims that were detached from dissolved shell substrate and interstitial sediment-filled molds can be quantified in thin-sections (Fig. 17).

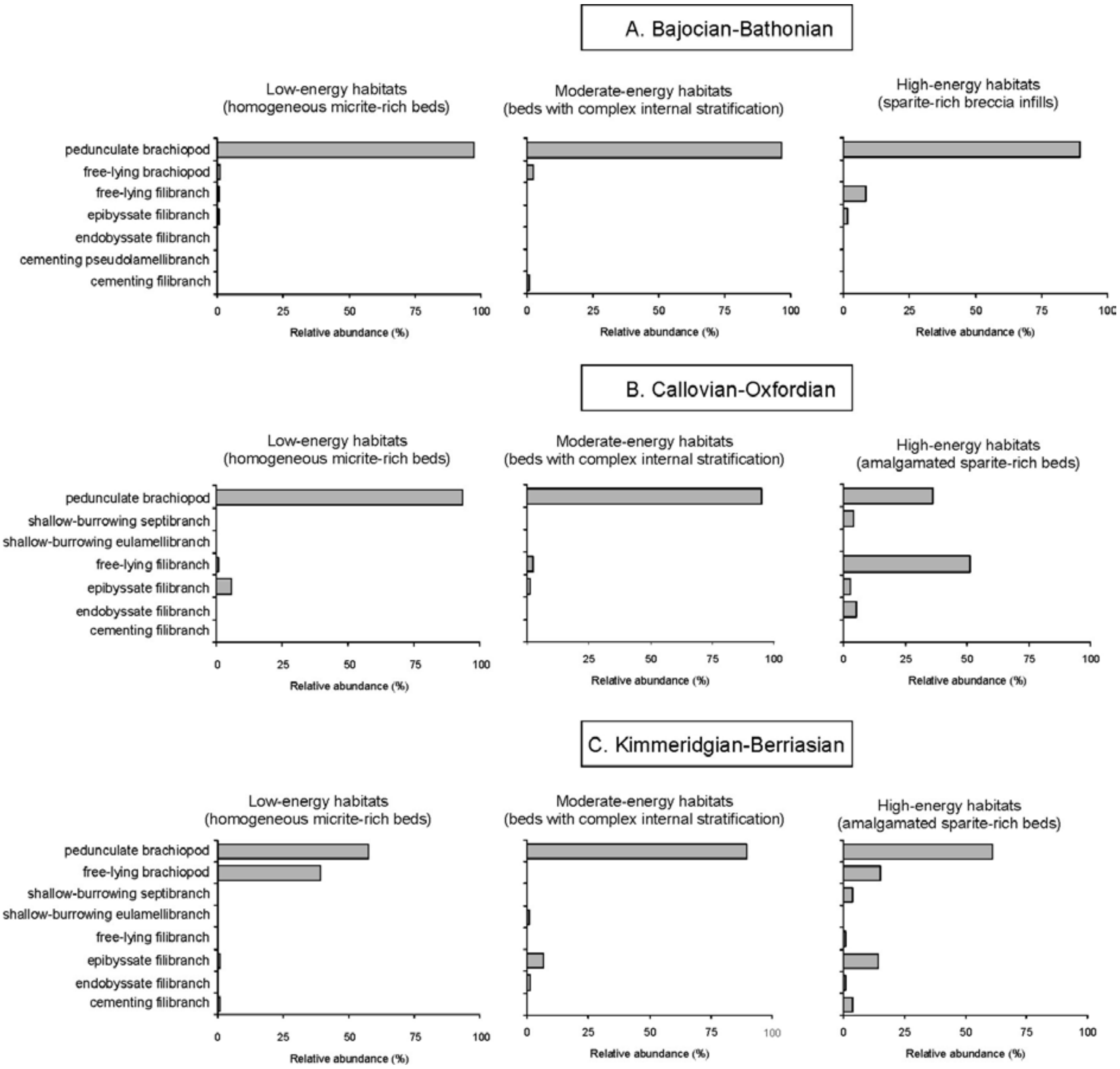


Figure 14 - Relative abundances of guilds in three habitats differing in the intensity of bottom currents during three time intervals. Note that abundance of bivalve guilds increases and abundance of brachiopods decreases towards high-energy habitats. A. Bajocian-Bathonian. B. Callovian-Oxfordian. C. Kimmeridgian-Berriasian.

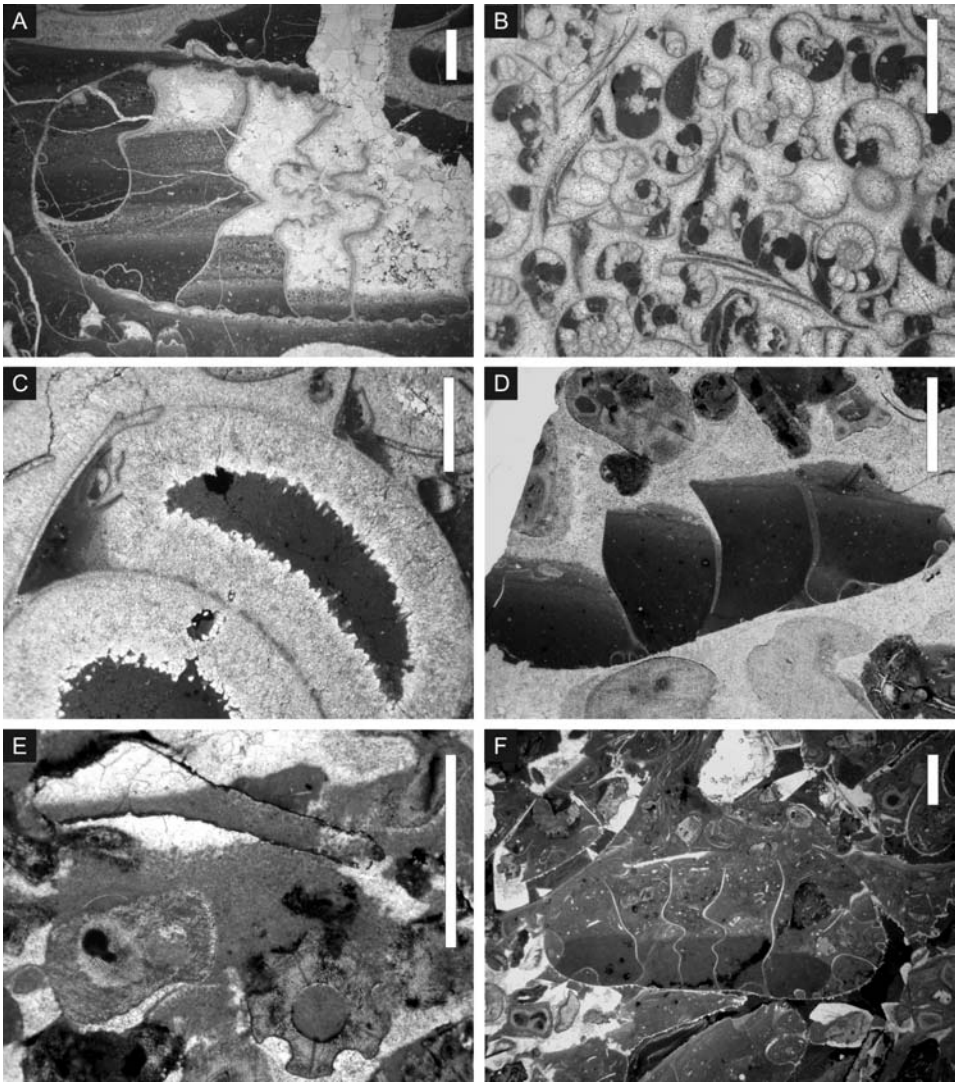


Figure 15 – Preservation of ammonites in thin-sections of the Štepnica and Bohunice formations (Štepnická skala section). A. Well-preserved ammonite shell with multiphase laminated infillings in rudstone. The shell is not coated by Fe-rims and shows no signs of dissolution. B. Shell concentration with well preserved juvenile ammonites. Note absence of Fe-coatings. C. Radiaxial fibrous calcite within chambers of an ammonite is overlain by micrite, indicating rapid calcite cementation in the taphonomic active zone. D. Fragment of an ammonite shell with dissolved septa replaced by interstitial micrite. E. An originally aragonitic mollusk fragment was coated by Fe. After the dissolution, the empty shell wall was infilled by interstitial micritic sediment. F. Ammonite shell with signs of dissolution in its upper part. Scale bars: 2 mm.

High proportions of ammonites with signs of dissolution and Fe-coatings occur in micrite-rich wackestones, floatstones and packstones of the Štepnica, Bohunice and Dursztyn formations. In contrast, ammonites from sparite-rich shell concentrations (rudstones) show rarely signs of dissolution and Fe-coatings (Fig. 17). This pattern holds true both for rudstones from the Callovian-Oxfordian and the Kimmeridgian-Berriasian (no data are available from Bajocian-Bathonian rudstones). Shell concentrations have a sharp basal boundary and show signs of grading. To evaluate the potential bias against less durable aragonitic taxa, guild abundances in taphofacies less affected by dissolution (i.e., rudstones) were separately computed for each time interval. It follows that the dominance of pedunculate brachiopods and epifaunal bivalves is still the typical feature of the macrobenthic communities of the PKBB in each time intervals (Fig. 18).

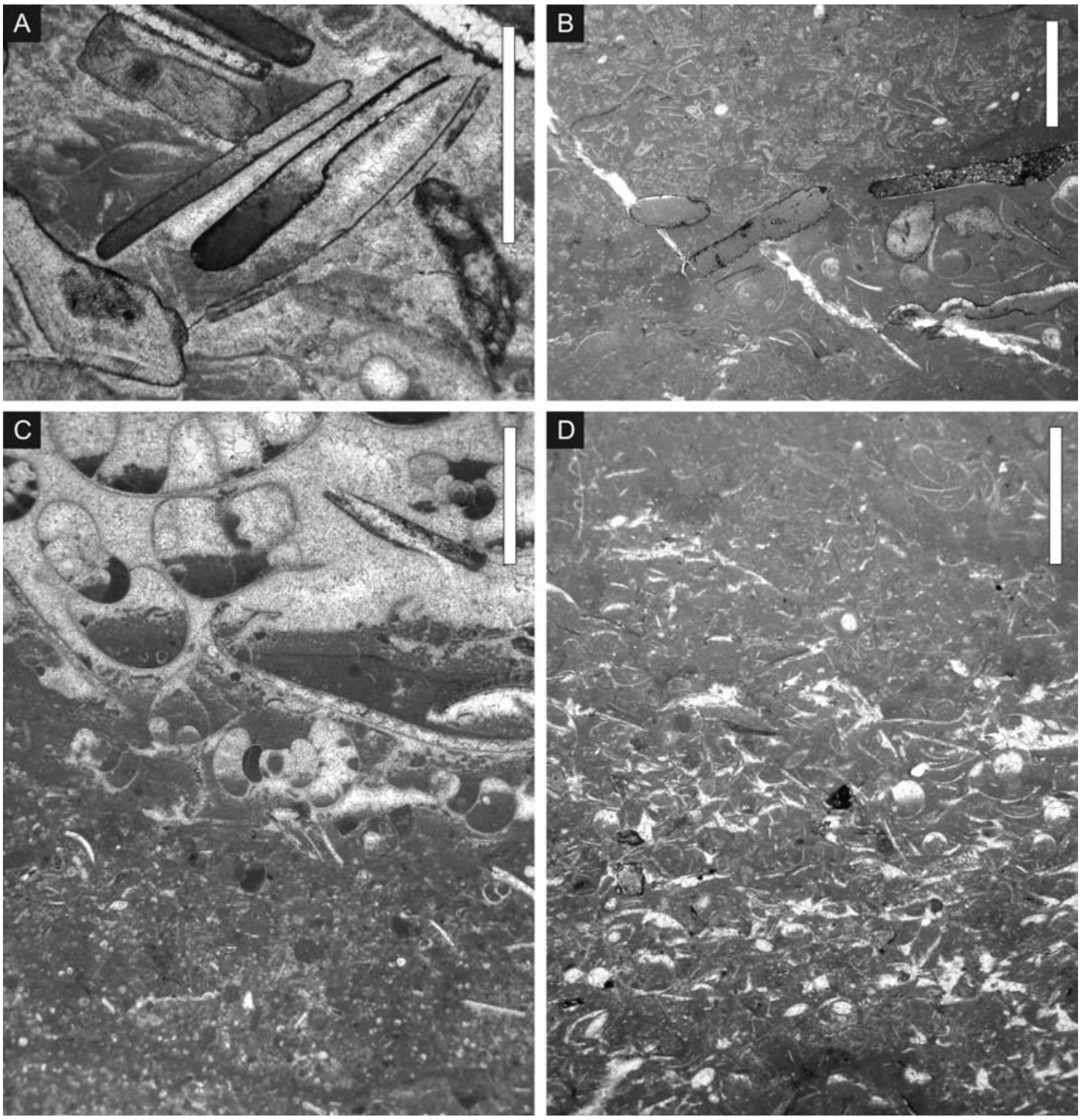


Figure 16 - Preservation of ammonites of the Dursztyn (A-B, D) and Bohunice formations (C). A. Dissolved ammonite relicts coated by Fe and partly infilled with interstitial micrite. B. Small-scale stratigraphic replacement of microfacies with juvenile ammonites (lower part) by *Saccocoma*-rich microfacies (upper part). C. A 2 cm-thick layer with radiolarians is abruptly replaced by ammonite rudstone. D. Graded packstone with juvenile ammonites. Scale bars: 2 mm.

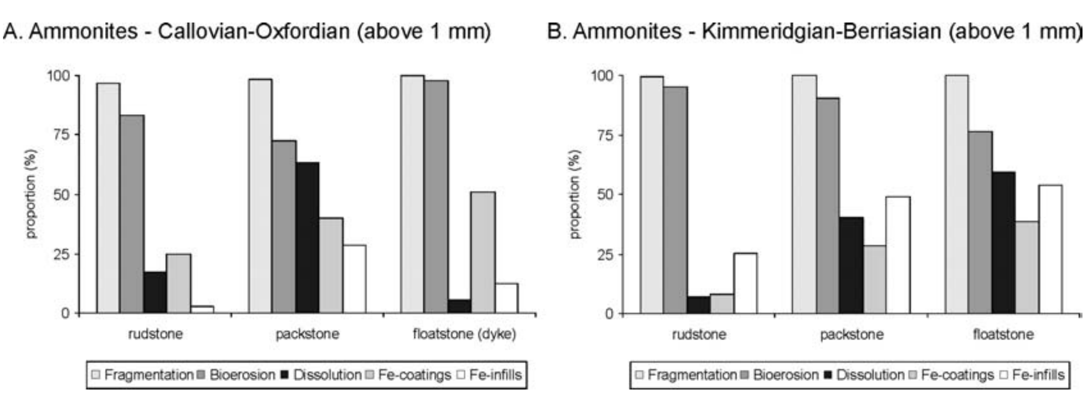


Figure 17 – Relative proportions of taphonomic variables scored on ammonites in thin-sections. Note the lower proportion of dissolved shells in rudstones in contrast to floatstones and packstones (Callovian-Oxfordian floatstones are derived from sedimentary dykes and show also low proportions of dissolved shells). Compositional fidelity of assemblages from rudstones is probably less affected by differential destruction of aragonitic taxa than fidelity of micrite-rich deposits. A. Callovian-Oxfordian ammonites. B. Kimmeridgian-Berriasian ammonites.

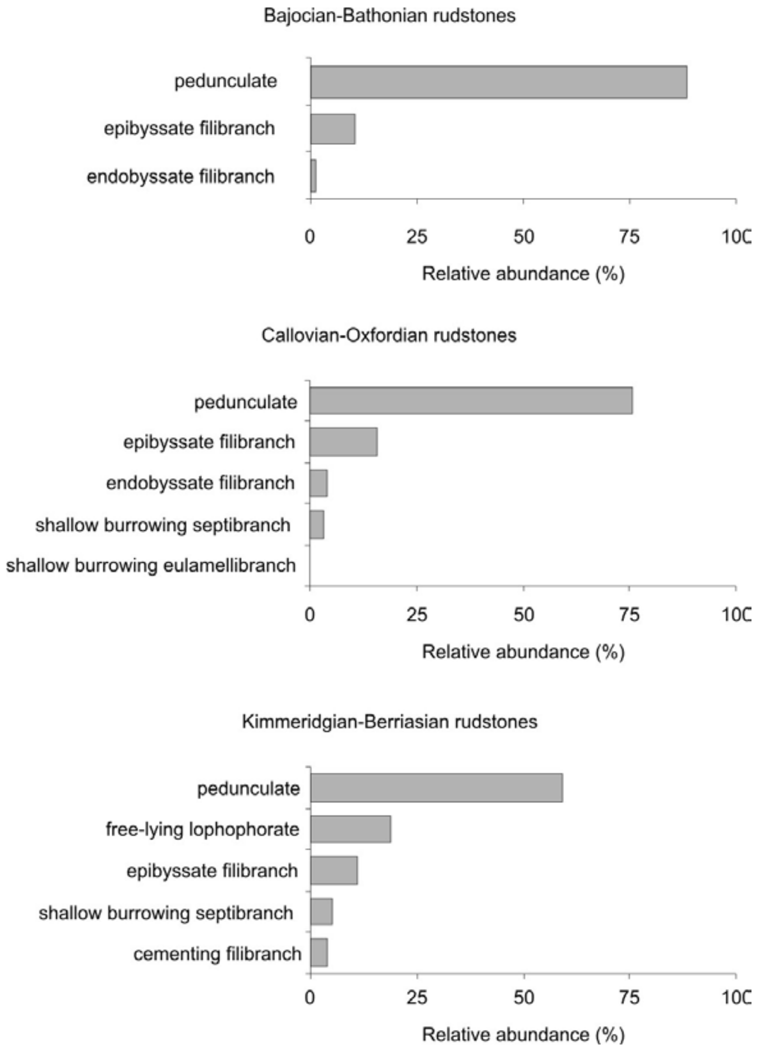


Figure 18 – Guild abundances in rudstones with low proportions of altered shells indicate that the guild structure dominated by pedunculate brachiopods and epifaunal bivalves is not caused by taphonomic bias against less durable aragonitic taxa.

Discussion

Guild structure – real or apparent? The uniform guild structure dominated by brachiopods and epifaunal bivalves with absence or rarity of semi-infaunal and infaunal bivalves is intriguing. Differential durability of calcitic, mostly epifaunal and aragonitic, mostly infaunal macrobenthic taxa, can be the inevitable explanation because sedimentologic evidence demonstrates preferential aragonite dissolution and calcite precipitation in the taphonomic active zone even in the shallowest habitats. The dominance of more durable calcitic taxa is completely in accord with the outcome of *strong* taphonomic filter against less durable aragonitic taxa (Behrensmeyer et al., 2005). This may indicate that the observed guild structure has a very low compositional fidelity and is biased towards a dominance of calcitic taxa. However, high abundance of ammonites, which represent a taphonomic control group of aragonitic bivalves, provides some circumstantial evidence for testing the possibility that the original communities were also dominated by calcitic taxa. The evaluation of guild abundances from shell concentrations that were affected by minor dissolution demonstrates that the guild structure is not strongly biased. Although it can be argued that a large proportion of aragonite shells was also dissolved in the rudstones but left no track in sediment, this option is less probable because formation of Fe-coatings took place on exposed shells and thus preceded dissolution of shells within the sediment. In addition, shell concentrations can buffer acid-rich pore-waters, thus possibly inhibiting or decreasing dissolution rates in comparison to sea-floors with dispersed shells. It is probable that shell concentrations with ammonites reflect single exhumation/burial events, leading to short exposure times of ammonite shells. In contrast, shell-poor wackestones and floatstones rather reflect background sedimentation, leading to high exposure times and higher dissolution of ammonite shells.

Guild structure of the Jurassic pelagic platform communities. It is important to note that in spite of the substantial taxonomic temporal turnover since the Middle Jurassic until the earliest Cretaceous, the guild structure dominated by brachiopods and epifaunal bivalves remained rather constant during this period. Such a guild structure was reported also from other Jurassic pelagic carbonate platforms of the Western Tethys. Mass occurrences of brachiopods represented by shell concentrations are known from the Lower Jurassic Hierlatz Formation of the Eastern Alps (Vörös, 1991), Middle Jurassic Klaus Formation of the Eastern Alps (Oppel, 1863), and the uppermost Jurassic-lowermost Cretaceous Dursztyn Formation of the Polish part of the PKBB (Krobicki, 1994). In terms of bivalve abundance, Sinemurian benthic communities of the Hierlatz Formation (Eastern Alps) were dominated by epibyssate and free-lying bivalves (Vörös et al., 2003). The Middle Jurassic pelagic platforms of the Transdanubian Central Range were dominated by epibyssate bivalves (Szente, 1995a), and other bivalve guilds were subordinate. Bivalves from red nodular marly deposits (Bathonian) of the Mecsek Mts. (Hungary) were represented mainly by epibyssate filibranchs (Vörös, 1995; Szente, 1995b). The Middle Jurassic pelagic platform deposits and sedimentary dykes of the Apennines, Alps and Carpathians contain monospecific shell concentrations of *Bositra buchi* (Sturani, 1967; Conti and Monari, 1992). Sturani (1971) found that Bajocian benthic communities of the Venetian Alps were dominated by *Bositra*, cementing and epibyssate bivalves, and brachiopods. Lower-Middle Jurassic deposits of western Sicily were dominated by brachiopods, *Bositra*, epibyssate and free-lying bivalves (Wendt, 1971), although deposit-feeding scaphopods and nuculid bivalves were locally also common. Heterodont bivalves constituted only 5% of all bivalves.

In some cases, gastropods were also common on pelagic carbonate platforms in terms of numerical abundance. Conti and Fischer (1982), Conti and Monari (1984) and Conti and Szabó (1987) described community relicts dominated by gastropods and epibyssate bivalves from Middle Jurassic deposits and sedimentary dykes of the Transdanubian Central Range and Umbria. Some Callovian dykes of the Czorsztyn pelagic platform were also inhabited by numerous gastropods (Uhlig, 1881). Although it is probable that benthic communities varied to some degree with fluctuating environmental factors, the guild structure with varying proportions of brachiopods and epifaunal bivalves (inclusing *Bositra* with weak byssal attachment) seems to be typical of the Jurassic pelagic carbonate platforms. This distinct guild structure points to specific ecologic preferences of benthic taxa that colonized such habitats.

Effects of substrate consistency. Although there are poor differences in guild abundances among soft, mixed and hard substrates, semi-infaunal and infaunal bivalves were rare on all of them. The dominance of epifaunal brachiopods and epibyssate bivalves might be partly driven by substrate properties that were unfavourable for semi-infaunal and infaunal bivalves (Fürsich, 1976; Kidwell and Jablonski, 1983; Fürsich et al., 1991). Sedimentologic evidence from pelagic carbonate sequences commonly indicates reduced sedimentation rates or omission and rapid lithification (e.g., combined effects of aragonite dissolution and rapid calcite cementation, concentrations of shells, formation of hardgrounds, sedimentary dykes, biostratigraphic condensation, and reduced sediment thickness as compared to deep basinal settings). In the Czorsztyn Unit, distinct mm-scale bioturbation is represented by simple burrows with differential sediment or sparite infillings in micrite-rich deposits. In addition, irregular spacing of bioclastic debris in shell-rich deposits indicates also some burrowing activity. However, preservation of cm-scale internal stratification with alternation of background and event deposits in all formations demonstrates that the intensity of bioturbation was negligible. Firm substrate can thus be one of the factors responsible for the distinct guild structure of brachiopod-bivalve communities on pelagic carbonate platforms.

Effects of bottom currents. Variations in the intensity of bottom currents were probably an important factor directly or indirectly determining distribution patterns of benthic taxa because on the scale of the Czorsztyn pelagic platform, brachiopods decreased and bivalves increased in abundance with increasing intensity of bottom currents during all time intervals. With respect to the intensity of bottom currents, present-day brachiopods and bivalves generally seem to show differential, non-monotonic response to varying flow speeds. Brachiopods create totally laminar flow during their feeding and any turbulence in their flow path represents increased feeding costs (LaBarbera, 1981b). Epifaunal bivalves might be better adapted to higher current velocities than brachiopods because their higher pumping and clearance rates are expected to be at optimum at higher flow speeds (Ackerman and Nishizaki, 2004) than lower pumping and clearance rates of brachiopods. The cost of suspension-feeding may thus be substantially higher for bivalves than for brachiopods under reduced flow speeds. In turn, high flow speeds can be less optimal for brachiopods with lower pumping rates. High flow speeds lead to deformation of filtering structures, high pressure differential between the inhalant and exhalant currents, and drag effects decreasing efficiency of particle selection and processing (Eckman and Duggins, 1993; Wildish et al., 1987). Brachiopods thus may have a higher feeding efficiency in low-energy habitats than epifaunal bivalves that tend to maximize the rate of water transport during their feeding (LaBarbera, 1981b).

Response of brachiopods and bivalves to food supply. Garrison and Fischer (1969) and Hallam (1975) suggested that rarity of macrobenthic fauna on pelagic carbonate platforms and basins of the western Tethys was caused by limited food supply because of remote physiographic and bathymetric position of the pelagic platforms with respect to coastal runoff and sea surface primary productivity. In accord with this, abundance of the Early Jurassic macrobenthos increased with decreasing depth on the pelagic platform of the Transdanubian Central Range (Vörös, 1973; Vörös, 1986). Abundance of Tithonian-Berriasian brachiopods similarly increased towards shallower parts of the Czorsztyn pelagic platform in the Polish part of the PKBB (Golonka and Krobicki, 2001). Although Golonka and Krobicki (2001) assumed that wind-driven upwelling might have occurred near the southern slopes of the Czorsztyn Ridge, the increasing abundance of brachiopods towards shallower habitats might be caused alone by (1) depth-dependent decrease in export production from sea surface productivity (cf., Gage and Tyler, 1991; Hay, 1995), and/or (2) an enhanced flow regime near topographic barriers represented by platform slopes and edges that tend to trap nutrients. The latter effect alone can also lead to localized upwelling of water because the pelagic platforms themselves could deflect deep currents similarly as present-day chains of seamounts.

On the scale of the Czorsztyn pelagic platform, the environmental segregation of brachiopods and epifaunal bivalves along a gradient with varying bottom currents probably correlated with a varying flux of food supply. With respect to the amount of food, both epifaunal bivalves with filibranch gills and brachiopods are able to cope with limited food supply. Actualistic evidence indicates that both groups can perform well under food-poor conditions (Rhodes and Thompson, 1992, 1993). However, food flux positively correlates with flow speeds, and it might be expected that with decreasing flow speeds, all other factors being constant, brachiopods were better adapted to conditions with reduced food supply than epifaunal bivalves. Environmental preferences of *Bositra* and dyscoliid brachiopods (e.g., *Pygope*) may indicate that the Jurassic brachiopods could have inhabited environments with less food supply than epifaunal bivalves. The preference of *Bositra* for habitats with higher food supply seems to be reasonable because adult *Bositra* reached its abundance peak in siliciclastic oxygen-deficient environment of the European shelf rather than in carbonate habitats of the western Tethys. *Bositra* that forms a constant rock-forming component of the Middle Jurassic pelagic platforms of the western Tethys does not typically exceed 1-2 mm in size and its abundance may correspond to progenetic holopelagic adults or unsuccessful settlement of teleplanic larvae (Oschmann, 1994). Zempolich (1993) assumed that mass occurrences of *Bositra buchi* in the Bajocian deposits of the Venetian Alps correspond to eutrophic events, possibly coupled with oxygen deficiency. Marked fluctuations in abundance of benthic adults and concentrations of juveniles and/or progenetic adults of *Bositra* thus can indicate unstable and fluctuating trophic regime with temporal peaks in sea surface productivity.

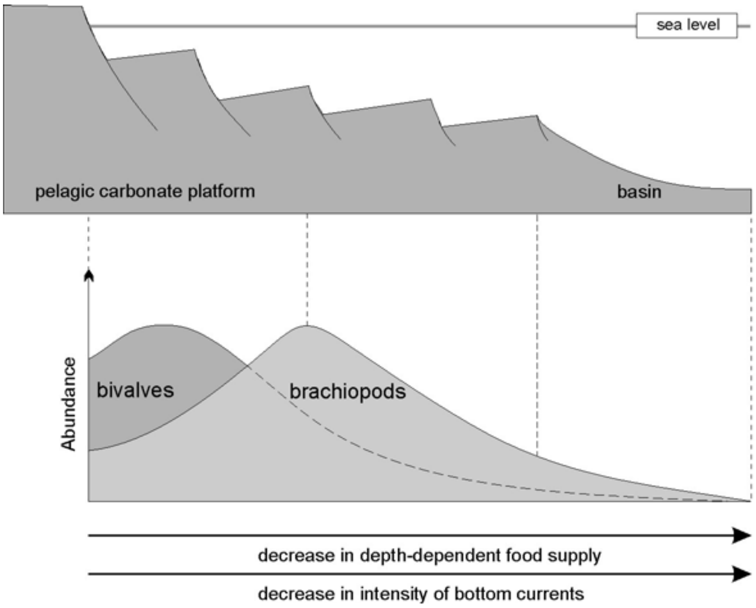


Figure 19 – Hypothesized response curves of brachiopods and epifaunal bivalves to simplified variations in intensity of bottom currents and food supply along a bathymetric transect across the pelagic carbonate platform and basin of the Pieniny Klippen Belt.

On the scale of the PKBB, brachiopods and bivalves occurred mainly in shallower environments of the pelagic platform tops and slopes (Czorsztyn and Pruské units). They were less common in slope-basin transition (Czertezik Unit) and very rare in the basin. The sulcate terebratulid brachiopods *Nucleata*, *Pygope* and *Pygites* belong to the few taxa that occurred also in basin habitats during the Late Jurassic-Early Cretaceous. The unique morphology of sulcate and bilobate terebratulids, including efficient separation of exhalant and inhalant currents, long anterior gape, large surface area of exposed mantle margin and good reorientation ability, is interpreted as a possible adaptation to reduced intensity of bottom currents, limited food supply, and limited oxygen concentrations (Ager, 1965; Vogel, 1966; Michalík, 1996; Kázmér, 1998). Both platform-scale and PKBB-scale patterns thus show that brachiopods preferred deeper or lower-energy habitats with lesser particulate flux than epifaunal bivalves (Fig. 19). The ability of brachiopods to dominate over epifaunal bivalves on the Jurassic pelagic platforms might thus be related to their better efficiency of food exploitation in habitats with moderate currents and low, albeit not the lowest food supply. The prediction of this hypothesis is that pelagic platforms reaching into the photic zone (e.g., the pelagic platforms in the Apennines were inhabited by pennular zooxanthellate corals, Gill et al., 2004) or affected by higher intensity of bottom currents should harbour more abundant epifaunal bivalves than deeper pelagic platforms because of the increased turbulence and increased depth-dependent flux of food supply (Fig. 19).

Zooplankton blooms as evidence of eutrophic conditions? Blooms of zooplankton such as radiolarians recorded in basin and of juvenile bivalves and planktonic foraminifers near pelagic platform and slope indicate that sea surface water layers were, at least at times, affected by high phytoplankton abundance. Baumgartner (1997) and Bartolini et al. (1999) suggested that peaks in radiolarian abundance during the Jurassic of the western Tethys reflect eutrophic conditions with high nutrient (silica) input and high surface primary productivity. Bartolini and Cecca (1999) indicated that the beginning of radiolarite-rich deposition during the Middle Jurassic was related to a climatic change with increasingly warmer and more humid climate, higher runoff and higher release of CO2, causing a crisis in carbonate production in shallow environments due to eutrophication and calcification inhibition (i.e., hardgrounds and considerable stratigraphic gaps). Radiolarian limestones and radiolarites deposited in basinal environments of the PKBB during the Bathonian-Oxfordian thus may indicate intervals of high nutrient input and sea surface primary productivity (Baumgartner, 1997; Bartolini et al., 1999).

High zooplankton productivity apparently contrasts with the inferred low food supply available for benthos, but this is traditionally explained by minimum export production into a benthic boundary layer in deep-sea habitats (Garrison and Fischer, 1969). Phytoplankton blooms might be either strongly seasonal, followed by long starvation periods or export of phytoplankton from the photic zone was strongly limited due to intense zooplankton grazing and faecal pellet recycling still in the photic zone (Wassmann, 1998). Bartolini and Cecca (1999) implicitly assumed a high food supply into benthic habitats during the Middle Jurassic of the Apennines because they suggested that the increased primary productivity negatively affected *benthic* production of carbonate-producing phototrophic organisms. The decrease in net carbonate production is evidenced by hiatuses in shallow environments, deposition of radiolarites in deep environments and a positive excursion of $\delta^{13}C$ in the Lower Bajocian deposits. However, the increase in export production to benthic habitats alone should have rather positive effects on net carbonate production of heterotrophic organisms such as crinoids or benthic mollusks. Therefore, the decrease in net carbonate production was probably more affected by decreased biocalcification rates and increased rates of carbonate destruction, owing to a higher CO_2 release caused by increased submarine volcanic activity (Bartolini and Cecca, 1999), rather than by abundance of food supply in the benthic boundary layer.

Pelagic carbonate platforms as unique brachiopod habitats. Vörös (2005) suggested that smooth brachiopods dominating on pelagic carbonate platforms in the western Tethys belonged to clades whose descendants preferentially occupy bathyal and abyssal depths in present-day seas (e.g., Norelloidea, Basiliolidae, Dyscoliidae, Dallinidae). These brachiopods contrast morphologically and phylogenetically with Jurassic multicostate brachiopods that inhabited the NW European margin (Vörös, 1993). According to this hypothesis, certain brachiopod clades preferred deep-sea environments and were adapted to low food supply already during the Mesozoic. After environmental crises (e.g., perturbations associated with mass extinctions) extirpated brachiopods from shallow-water habitats, the surviving brachiopod clades in deep-sea habitats could invade shallow habitats of the pelagic carbonate platforms. This hypothesis assumes that either (1) colonization of shallow-water habitats by deep-sea brachiopods was enhanced by reduced biotic pressure because the former incumbents were removed from shallow-water environments after some perturbation, or (2) environmental conditions on intra-oceanic pelagic carbonate platforms were more comparable to deep-sea habitats than to continental shelf seas. Deep-sea brachiopod clades could thus track their preferred conditions into shallow habitats. Vörös (2005) noted that the success of brachiopods on shallow swells was restricted to times when oceans basins were closed on the west and characterized by specific circulation regime with westerly-oriented currents. He advocated combined effects of both scenarios because of rapid recovery of brachiopods on the shallow pelagic platforms after the end-Triassic and early-Toarcian mass extinctions (in contrast to slow recovery in NW Europe), and presumed low food supply in the western end of the Tethys (Vörös, 1973; Hallam, 1975). However, effects of these two scenarios can be distinguished. First, if removal of competitors enabled brachiopod colonization of shallow pelagic platforms, brachiopods should simply extend their bathymetric range towards shallow habitats and should still occur also in deep-sea environments. However, Jurassic brachiopods increased in their abundance towards shallow environments and were absent (during the Middle Jurassic) or less common (*Nucleata* and *Pygope* during the Late Jurassic/Early Cretaceous) in deep-sea environments of the western Tethys. Second, shallow-water survivors should be able to renew their original environmental ranges during a recovery phase, thus leading to elimination of fauna that colonized vacated shallow environments after perturbation. However, brachiopods continuously dominated on pelagic carbonate platforms during the whole Jurassic. Brachiopods were probably well adapted to environments with low, albeit not lowest, food supply along a gradient with varying productivity, implying that their success on shallow pelagic platforms was related to unique abiotic conditions (i.e., combination of substrate firmness and depth-dependent food supply) rather than to removal of shallow-water incumbents after extinction events and subsequent colonization of shallow habitats by deep-sea brachiopods.

Conclusions

(1) Brachiopod-bivalve communities of sediment-starved, pelagic carbonate platforms of the PKBB were characterized by a distinct guild structure with dominant pedunculate brachiopods and common epibyssate bivalves. Evidence for aragonite dissolution in the TAZ is indicated by interstitial sediment-filled ammonite molds, bored and encrusted molds and isolated Fe-rich coatings that were left free after dissolution of their aragonitic shell substrate. To test whether the guild structure is biased against less durable aragonitic bivalves, guild abundances were separately computed for simple-event shell concentrations with minimum signs of aragonite dissolution. It follows that such samples are also dominated by brachiopods and epifaunal bivalves, indicating that the guild structure is not *strongly* biased.

(2) Co-occurrence patterns of brachiopods and bivalves in each of three time intervals demonstrate that they significantly differ in their abundances, indicating their distinct environmental preferences. High firmness of substrate probably played the important role in exclusion of infaunal bivalves because sedimentologic features indicate very low sedimentation rates associated with rapid cementation of the sea-floor. Variations in substrate composition and intensity of bottom currents show a significant correlation with the composition of benthic communities on the scale of the Czorsztyn pelagic platform, indicating that brachiopods preferred deeper and low-energy habitats in contrast to epifaunal bivalves. In addition, some brachiopod clades were able to inhabit deeper habitats

than bivalves on the scale of the PKBB. The platform-scale and PKBB-scale patterns point to segregation of brachiopod and epifaunal bivalves along gradients with varying intensity of bottom currents and food supply. It is suggested that dominance of brachiopods over epifaunal bivalves on the shallow Jurassic pelagic platforms was enhanced by their better exploitation of low, albeit not the lowest food supply. The success of brachiopods on Jurassic shallow pelagic platforms was related to unique abiotic conditions rather than to extinction of shallow-water incumbents and subsequent colonization of shallow habitats by deep-sea brachiopods.

	MS11	MS03	SK-VR7	SK-VR17	SK-VR1	SK-VR22	SK-VR25	SK-VR38	SK-VR6	SK-VR47	VR-47	VR1	VR2	VR4	VR5	VR8	VR9	VR15	VR16	VR17
Acanthothiris spinosa	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Praelacunosella aff. *sublacunosa*	0	0	13	8	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0
Praelacunosella sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praelacunosella aff. *dumortieri*	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	20	7	0	0	0
Lacunosella monsalviensis	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Rhactorhynchia pallax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capillirhynchia aff. *furcillata*	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella agassizi	7	3	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Monticlarella capillata	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella rollieri	0	0	0	0	18	0	0	0	0	0	99	0	0	0	0	0	0	0	0	4
Monticlarella fascilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella aff. *triloboides*	0	0	0	0	0	0	60	21	0	0	0	0	0	4	4	0	0	0	0	0
Caucasella trigona	0	0	0	0	0	0	0	0	0	0	0	0	0	24	1	0	0	0	0	0
Apringia aff. *atla*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Striirhynchia subechinata	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	1	0	0	0
Striirhynchia brentoniaca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Septocrurella defluxa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Septocrurella sanctaeclarae	0	0	0	0	12	0	0	0	0	0	186	0	0	0	0	0	0	0	0	18
Rectirhynchia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Karadagithyris bilimeki	10	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Karadagithyris decipiens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11
Karadagithyris eduardi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Karadagithyris sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Monsardithyris ventricosa	0	0	0	0	0	0	0	0	0	0	0	0	0	30	30	0	0	0	0	0
Dundrythyris retrocarinata	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	3	38	0	0	0
Goniothyris hungarica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ferrithyris ferryi	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0
Antiptychina bivallata	0	0	0	0	0	0	0	0	0	0	0	0	0	5	32	0	0	0	0	0
Linguithyris bifida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linguithyris curviconcha	0	0	0	0	2	0	0	0	0	0	14	0	0	5	0	0	2	0	0	1
Linguithyris vicaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucleata planulata	9	6	0	0	0	0	0	0	5	0	0	1	4	0	0	0	0	0	0	0
Pygope diphya	26	10	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0
Pygope janitor	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygope catulloi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygites diphyoides	0	0	0	0	0	0	0	0	0	1	0	6	9	0	0	0	0	8	3	0
Triangope triangulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella moutoniformis	0	0	0	0	0	0	0	0	65	21	0	5	7	0	0	0	0	7	8	0
Aulacothyris sp.	0	0	0	0	0	0	0	0	0	0	81	0	0	0	20	0	0	0	0	3
Dictyothyropsis tatrica	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Zittelina pinguicula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina wahlenbergi	0	0	0	0	0	0	0	0	15	0	0	6	31	0	0	0	0	1	7	0
Zittelina beneckei	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria waltoni	0	0	11	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Bositra	0	0	0	2	0	0	0	0	0	0	0	0	0	13	6	0	0	0	0	0
Cuspidaria	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0
Placunopsis	2	1	0	1	0	2	0	0	0	0	9	0	1	0	0	0	0	0	0	0
Pseudolimea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spondylopecten	1	0	0	2	0	18	0	1	0	0	23	0	0	0	2	0	0	0	0	0
Propeamussium	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Camptonectes	1	1	0	7	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
Aucella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Inoceramus	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
Pteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma	1	1	2	2	0	12	1	0	0	0	37	0	0	0	0	0	0	0	0	0
Isoarca	0	1	0	0	0	0	0	0	0	0	21	0	0	1	0	0	0	0	0	0
Cardium	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
Protocardia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma	0	0	4	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meleagrinella	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys	0	0	14	4	0	9	5	2	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lopha	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 – Absolute abundances of brachiopod species and bivalve genera.

	Z05	Z12	Z17.2	Z18	SS4-09	SS5-05	SS1-46.2	SS2-17.5	SS2-28	SS2-28.6	SS2-28.5	SS2-28.8	SS2-29	SS2-32	SS3-25.5	SS3-26.2	SS3-27	SS3-23.3	SS3-23.9	SS3-22.9
Acanthothiris spinosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Praelacunosella aff. *sublacunosa*	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0
Praelacunosella sp.	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Praelacunosella aff. *dumortieri*	0	0	0	0	2	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella monsalviensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhactorhynchia pallax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Capillirhynchia aff. *furcillata*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella agassizi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella capillata	5	2	13	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella rollieri	0	0	0	0	13	18	0	0	24	3	7	7	6	4	48	6	10	3	27	16
Monticlarella fascilla	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella aff. *triloboides*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caucasella trigona	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	1	0	0	8	0
Apringia aff. *atla*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Striirhynchia subechinata	0	0	0	0	0	0	0	4	3	0	2	0	0	0	1	0	0	0	2	0
Striirhynchia brentoniaca	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Septocrurella defluxa	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Septocrurella sanctaeclarae	0	0	0	0	22	65	0	0	103	24	7	46	3	0	60	9	4	12	89	6
Rectirhynchia sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Karadagithyris bilimeki	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Karadagithyris decipiens	0	0	0	0	5	12	0	0	18	14	10	1	13	5	41	4	9	16	14	47
Karadagithyris eduardi	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0
Karadagithyris sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Zittelina sp. A	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Monsardithyris ventricosa	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Dundrythyris retrocarinata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Goniothyris hungarica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ferrithyris ferryi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Antiptychina bivallata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linguithyris bifida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linguithyris curviconcha	0	0	0	0	0	0	13	20	10	1	3	8	4	24	16	0	0	6	29	5
Linguithyris vicaria	0	0	0	0	6	0	0	0	42	16	45	11	8	0	45	6	9	11	17	3
Nucleata planulata	0	0	16	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygope diphya	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygope janitor	53	3	17	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygope catulloi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygites diphyoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triangope triangulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella moutoniformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulacothyris sp.	0	0	0	0	6	0	0	0	4	0	0	0	0	0	2	0	0	0	0	0
Dictyothyropsis tatrica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina pinguicula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina wahlenbergi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina beneckei	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria waltoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arca	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Bositra	0	0	0	0	0	5	0	2	10	1	17	0	34	2	0	0	0	0	0	0
Cuspidaria	0	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0
Placunopsis	0	1	1	4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pseudolimea	2	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spondylopecten	1	1	0	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Propeamussium	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Camptonectes	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Aucella	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Inoceramus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiostoma	0	0	5	5	10	0	1	1	0	0	0	0	0	2	1	0	0	0	0	0
Isoarca	0	0	2	1	0	0	2	0	0	0	0	0	0	9	0	0	0	0	0	0
Cardium	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Protocardia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Modiolus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Meleagrinella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lopha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 (cont.) – Absolute abundances of brachiopod species and bivalve genera.

	BA43	BE	KY1-32	KY1-34.1	KY1-34.21	ME05	ME07	PL16	S2-01	S2-02	S2-03	SS1-43	SS3-22
Acanthothiris spinosa	0	0	0	0	0	3	1	0	0	0	0	0	0
Praelacunosella aff. *sublacunosa*	24	1	0	0	0	8	4	0	0	0	0	0	0
Praelacunosella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Praelacunosella aff. *dumortieri*	0	0	0	0	0	0	0	0	0	0	0	0	0
Lacunosella monsalviensis	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhactorhynchia pallax	0	0	0	0	0	1	1	0	0	0	0	0	0
Capillirhynchia aff. *furcillata*	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella agassizi	0	0	1	0	0	0	0	4	0	3	0	0	0
Monticlarella capillata	0	0	0	0	0	0	0	0	0	0	3	0	0
Monticlarella rollieri	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella fascilla	0	0	0	0	0	0	0	0	0	0	0	0	0
Monticlarella aff. *triloboides*	0	0	0	0	0	0	0	0	0	0	0	0	0
Caucasella trigona	4	0	0	0	0	0	0	0	0	0	0	0	0
Apringia aff. *atla*	0	4	0	0	0	0	0	0	0	0	0	0	0
Striirhynchia subechinata	0	0	0	0	0	0	0	0	0	0	0	0	0
Striirhynchia brentoniaca	0	0	0	0	0	0	0	0	0	0	0	0	0
Septocrurella defluxa	0	0	0	0	0	0	0	0	0	0	0	0	0
Septocrurella sanctaeclarae	0	0	0	0	0	0	0	0	0	0	0	0	0
Rectirhynchia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Karadagithyris bilimeki	0	0	6	1	1	0	0	3	1	0	1	0	0
Karadagithyris decipiens	0	0	0	0	0	0	0	0	0	0	0	0	0
Karadagithyris eduardi	6	4	0	0	0	0	0	0	0	0	0	0	0
Karadagithyris sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
Monsardithyris ventricosa	39	0	0	0	0	0	1	0	0	0	0	0	0
Dundrythyris retrocarinata	0	0	0	0	0	14	11	0	0	0	0	0	0
Goniothyris hungarica	0	0	0	0	0	3	9	0	0	0	0	0	0
Ferrithyris ferryi	0	0	0	0	0	0	0	0	0	0	0	0	0
Antiptychina bivallata	10	0	0	0	0	0	0	0	0	0	0	0	0
Linguithyris bifida	0	0	0	0	0	8	6	0	0	0	0	0	0
Linguithyris curviconcha	13	10	0	0	0	0	0	0	0	0	0	0	0
Linguithyris vicaria	0	0	0	0	0	0	0	0	0	0	0	0	0
Nucleata planulata	0	0	0	1	0	0	0	3	0	0	0	0	0
Pygope diphya	0	0	16	14	22	0	0	1	16	10	32	0	0
Pygope janitor	0	0	0	0	0	0	0	20	6	5	3	0	0
Pygope catulloi	0	0	0	0	0	0	0	0	0	0	0	0	0
Pygites diphyoides	0	0	0	0	0	0	0	0	0	0	0	0	0
Triangope triangulus	0	0	0	0	0	0	0	0	2	0	0	0	0
Lacunosella moutoniformis	0	0	0	0	0	0	0	0	0	0	0	0	0
Aulacothyris sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Dictyothyropsis tatrica	0	0	0	0	0	0	0	0	0	0	0	0	0
Zittelina pinguicula	0	0	0	9	0	0	0	0	0	0	0	0	0
Zittelina wahlenbergi	0	0	0	0	28	0	0	0	0	0	2	0	0
Zittelina beneckei	0	0	0	0	0	0	0	0	0	0	0	0	0
Zeilleria waltoni	0	0	0	0	0	5	2	0	0	0	0	0	0
Zeilleria sp. A	0	0	0	0	0	2	2	0	0	0	0	0	0
Arca	0	0	0	0	0	0	0	0	0	0	0	0	0
Bositra	0	0	0	0	0	0	0	0	0	0	0	50	50
Cuspidaria	0	0	1	7	0	0	0	0	0	0	0	0	0
Placunopsis	0	0	1	3	1	0	1	0	0	0	0	0	0
Pseudolimea	0	0	2	0	0	0	0	0	0	0	0	0	0
Spondylopecten	0	0	7	0	0	0	0	1	0	0	0	0	0
Propeamussium	0	0	0	2	0	0	0	0	0	0	0	0	0
Camptonectes	0	0	0	1	1	0	0	0	0	0	0	0	0
Aucella	0	0	0	0	0	0	0	0	0	0	0	0	0
Entolium	0	0	0	0	0	0	0	0	0	0	0	0	0
Eopecten	0	0	0	3	0	0	0	0	0	0	0	0	0
Inoceramus	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteria	0	0	0	0	0	1	0	0	0	0	0	0	0
Plagiostoma	1	0	1	0	0	0	0	0	0	0	0	0	0
Isoarca	0	0	1	0	0	0	0	0	0	0	1	0	0
Cardium	0	0	0	0	0	0	0	0	0	0	0	0	0
Protocardia	0	0	0	0	0	0	0	1	0	0	0	0	0
Modiolus	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxytoma	0	0	0	0	0	0	0	0	0	0	0	0	0
Meleagrinella	0	0	0	0	0	0	0	0	0	0	0	0	0
Chlamys	0	0	0	0	0	0	0	0	0	0	0	0	0
Plicatula	0	0	0	0	0	0	0	0	0	0	0	0	0
Ctenostreon	0	0	0	0	0	0	0	0	0	0	0	0	0
Lopha	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1 (cont.) – Absolute abundances of brachiopod species and bivalve genera.

Sample	Formation	Age	Substrate	Water energy
MS11	Rogoznik Limestone	Tithonian	hard-bottom	amalgamation
MS03	Rogoznik Limestone	Tithonian	soft-bottom	homogeneous
SK-VR7	Krupianka Limestone	Bajocian/Bathonian	mixed-bottom	no data
SK-VR17	Krupianka Limestone	Bajocian/Bathonian	mixed-bottom	no data
SK-VR1	Stepnica Limestone	Oxfordian	soft-bottom	homogeneous
SK-VR22	Vrsatec Limestone	Bajocian/Bathonian	hard-bottom	coral framework
SK-VR25	Vrsatec Limestone	Bajocian/Bathonian	hard-bottom	no data
SK-VR38	Vrsatec Limestone	Bajocian/Bathonian	hard-bottom	no data
SK-VR6	Rogoznik Limestone	Berriasian	mixed-bottom	homogeneous
SK-VR47	Rogoznik Limestone	Berriasian	mixed-bottom	homogeneous
VR-47	Stepnica Limestone	Oxfordian	mixed-bottom	complex structure
VR1	Rogoznik Limestone	Berriasian	mixed-bottom	homogeneous
VR2	Rogoznik Limestone	Berriasian	mixed-bottom	homogeneous
VR4	Vrsatec Limestone	Bajocian/Bathonian	hard-bottom	amalgamation
VR5	Vrsatec Limestone	Bajocian/Bathonian	hard-bottom	amalgamation
VR8	Krupianka Limestone	Bajocian/Bathonian	mixed-bottom	complex structure
VR9	Krupianka Limestone	Bajocian/Bathonian	mixed-bottom	complex structure
VR15	Rogoznik Limestone	Berriasian	mixed-bottom	homogeneous
VR16	Rogoznik Limestone	Berriasian	mixed-bottom	homogeneous
VR17	Stepnica Limestone	Callovian/Oxfordian	soft-bottom	homogeneous
Z05	Rogoznik Limestone	Tithonian	mixed-bottom	complex structure
Z12	Rogoznik Limestone	Tithonian	mixed-bottom	homogeneous
Z17.2	Rogoznik Limestone	Kimmeridgian/Tithonian	hard-bottom	complex structure
Z18	Rogoznik Limestone	Kimmeridgian/Tithonian	hard-bottom	amalgamation
SS4-09	Stepnica Limestone	Callovian	soft-bottom	homogeneous
SS5-05	Stepnica Limestone	Bathonian/Callovian	hard-bottom	complex structure
SS1-46.2	Bohunice Limestone	Oxfordian	hard-bottom	amalgamation
SS2-17.5	Czorsztyn Limestone	Bathonian	soft-bottom	homogeneous
SS2-28	Stepnica Limestone	Bathonian/Callovian	hard-bottom	complex structure
SS2-28.6	Stepnica Limestone	Bathonian/Callovian	hard-bottom	complex structure
SS2-28.5	Stepnica Limestone	Bathonian/Callovian	hard-bottom	complex structure
SS2-28.8	Stepnica Limestone	Bathonian/Callovian	mixed-bottom	complex structure
SS2-29	Stepnica Limestone	Bathonian/Callovian	hard-bottom	amalgamation
SS2-32	Bohunice Limestone	Oxfordian	hard-bottom	amalgamation
SS3-25.5	Stepnica Limestone	Bathonian/Callovian	mixed-bottom	complex structure
SS3-26.2	Stepnica Limestone	Bathonian/Callovian	mixed-bottom	complex structure
SS3-27	Stepnica Limestone	Bathonian/Callovian	mixed-bottom	complex structure
SS3-23.3	Stepnica Limestone	Bathonian/Callovian	mixed-bottom	complex structure
SS3-23.9	Stepnica Limestone	Bathonian/Callovian	mixed-bottom	complex structure
SS3-22.9	Stepnica Limestone	Bathonian/Callovian	mixed-bottom	complex structure
BA43	Bohunice Limestone	Bathonian	mixed-bottom	homogeneous
BE	Czorsztyn Limestone	Bathonian	mixed-bottom	homogeneous
KY1-32	Rogoznik Limestone	Tithonian	hard-bottom	amalgamation
KY1-34.1	Rogoznik Limestone	Berriasian	hard-bottom	amalgamation
KY1-34.21	Rogoznik Limestone	Berriasian	hard-bottom	amalgamation
ME05	Krupianka Limestone	Bajocian	mixed-bottom	complex structure
ME07	Krupianka Limestone	Bajocian	mixed-bottom	complex structure
PL16	Rogoznik Limestone	Tithonian	mixed-bottom	complex structure
S2-01	Rogoznik Limestone	Kimmeridgian/Tithonian	mixed-bottom	homogeneous
S2-02	Rogoznik Limestone	Kimmeridgian/Tithonian	mixed-bottom	homogeneous
S2-03	Rogoznik Limestone	Kimmeridgian/Tithonian	mixed-bottom	homogeneous
SS1-43	Stepnica Limestone	Bathonian/Callovian	hard-bottom	amalgamation
SS3-22	Czorsztyn Limestone	Bathonian/Callovian	hard-bottom	amalgamation

Appendix 2 – Environmental and stratigraphic assignments.

Taxon	Guild
Acanthothiris spinosa	pedunculate brachiopod
Praelacunosella aff. *sublacunosa*	pedunculate brachiopod
Praelacunosella sp.	pedunculate brachiopod
Praelacunosella aff. *dumortieri*	pedunculate brachiopod
Lacunosella monsalviensis	pedunculate brachiopod
Rhactorhynchia pallax	pedunculate brachiopod
Capillirhynchia aff. *furcillata*	pedunculate brachiopod
Monticlarella agassizi	pedunculate brachiopod
Monticlarella capillata	pedunculate brachiopod
Monticlarella rollieri	pedunculate brachiopod
Monticlarella fascilla	pedunculate brachiopod
Monticlarella aff. triloboides	pedunculate brachiopod
Caucasella trigona	pedunculate brachiopod
Apringia aff. *atla*	pedunculate brachiopod
Striirhynchia subechinata	pedunculate brachiopod
Striirhynchia brentoniaca	pedunculate brachiopod
Septocrurella defluxa	pedunculate brachiopod
Septocrurella sanctaeclarae	pedunculate brachiopod
Rectirhynchia sp.	pedunculate brachiopod
Karadagithyris bilimeki	pedunculate brachiopod
Karadagithyris decipiens	pedunculate brachiopod
Karadagithyris eduardi	pedunculate brachiopod
Karadagithyris gerda	pedunculate brachiopod
Karadagithyris sp. A	pedunculate brachiopod
Zittelina sp. A	free-lying brachiopod
Monsardithyris ventricosa	pedunculate brachiopod
Dundrythyris retrocarinata	pedunculate brachiopod
Goniothyris hungarica	pedunculate brachiopod
Ferrithyris ferryi	pedunculate brachiopod
Antiptychina bivallata	pedunculate brachiopod
Linguithyris bifida	pedunculate brachiopod
Linguithyris curviconcha	pedunculate brachiopod
Linguithyris vicaria	pedunculate brachiopod
Nucleata planulata	pedunculate brachiopod
Pygope diphya	pedunculate brachiopod
Pygope janitor	pedunculate brachiopod
Pygope catulloi	pedunculate brachiopod
Pygites diphyoides	pedunculate brachiopod
Triangope triangulus	pedunculate brachiopod
Lacunosella moutoniformis	free-lying brachiopod
Aulacothyris sp.	pedunculate brachiopod
Dictyothyropsis tatrica	pedunculate brachiopod
Zittelina pinguicula	free-lying brachiopod
Zittelina wahlenbergi	free-lying brachiopod
Zittelina beneckei	free-lying brachiopod
Zeilleria waltoni	pedunculate brachiopod
Zeilleria sp. A	pedunculate brachiopod
Arca	epibyssate filibranch
Bositra	free-lying filibranch
Cuspidaria	shallow burrowing septibranch
Placunopsis	cementing filibranch
Pseudolimea	epibyssate filibranch
Spondylopecten	epibyssate filibranch
Propeamussium	free-lying filibranch
Camptonectes	epibyssate filibranch
Aucella	epibyssate filibranch
Entolium	free-lying filibranch
Eopecten	epibyssate filibranch
Inoceramus	epibyssate filibranch
Pteria	epibyssate filibranch
Plagiostoma	epibyssate filibranch
Isoarca	shallow burrowing protobranch
Cardium	shallow burrowing eulamellibranch
Protocardia	shallow burrowing eulamellibranch
Modiolus	endobyssate filibranch
Oxytoma	epibyssate filibranch
Meleagrinella	epibyssate filibranch
Entolium	free-lying filibranch
Propeamussium	free-lying filibranch
Camptonectes	epibyssate filibranch
Chlamys	epibyssate filibranch
Eopecten	epibyssate filibranch
Plicatula	cementing filibranch
Placunopsis	cementing filibranch
Ctenostreon	epibyssate filibranch
Plagiostoma	epibyssate filibranch
Pseudolimea	epibyssate filibranch
Lopha	cementing pseudolamellibranch

Appendix 3 – Guild assignments.

13. Summary

Non-random environmental segregation of brachiopod and bivalve communities consistently follows from analyses of the Upper Triassic and Jurassic datasets performed on local to regional, formation-level scales. R values based on Q-mode based analyses of similarities explicitly quantify environmental control on abundances of brachiopods and bivalves. Variations in siliciclastic supply, wave-base level and substrate consistency mostly showed significant effects on taxonomic and guild composition, although their effects can be confounded by interaction with other factors. Bivalves increased in abundance towards shallower environments with higher flow velocity and higher food supply and towards environments with higher terrigenous supply. In contrast, brachiopods increased in abundance towards deeper environments and towards environments with higher carbonate supply. This general differentiation either with respect to onshore-offshore gradient and/or to carbonate-siliciclastic gradient holds for the Upper Triassic environments of the Alps and Carpathians, the Lower and Middle Jurassic environments of the High Atlas, the Middle-Upper Jurassic environments of the West Carpathians, and the Upper Jurassic environments of the Swiss Jura and southern Germany. Such environmental differentiation does not automatically follow from the most obvious ecologic difference between brachiopods and bivalves, which is related to their differential substrate preferences (i.e., rhynchonelliformean brachiopods are poorly mobile and do not possess infaunal life habits). Although substrate consistency is also showing substantial effects on abundance of brachiopods and bivalves, epifaunal brachiopods were common inhabitants of soft-bottom habitats in the Late Triassic and Jurassic (although still with available substrates for attachment of juvenile and adult specimens). However, one exception to the pattern, represented by the Upper Oxfordian formations of the Swiss Jura where deep-shelf environments are dominated by infaunal bivalves and platform environments by brachiopods and epifaunal bivalves, can be caused by overriding effects of substrate varations and reduced effects of variations in flow velocity or food supply. In general, abundance peaks of brachiopods were reached either in (1) carbonate-rich, food-poor environments that were not affected by terrigenous supply and land-derived nutrients (e.g., onshore oolite bars, oncoidal and skeletal banks, and coral biostromes and bioherms of the Kössen, Fatra, Bin El Ouidane and Vellerat formations, and pelagic carbonate platforms of the Pieniny Klippen Belt), or in (2) offshore environments rich in nutrients and/or rich in terrigenous supply but temporally limited in flow velocity and possibly limited in oxygen concentrations (e.g., Early and Late Jurassic sponge-rich environments).

Similarity in abundance patterns between brachiopods and bivalves, as quantified by R values based on R-mode based analyses of similarities and by Bray-Curtis similarities, indicates that brachiopods consistently differ in abundance pattern from eulamellibranch, mainly infaunal bivalves. For datasets where number of brachiopods and eulamellibranchs possessed more than three species, this difference was invariably significant This is true of the Kössen Formation ($R = 0.33$, $p < 0.0001$), the Fatra Formation ($R = 0.45$, $p = 0.0095$), the Hybe Formation ($R = 0.41$, $p = 0.001$), the Bajocian formations of the High Atlas ($R = 0.37$, $p = 0.0002$), and the Upper Oxfordian formations of the Swiss Jura ($R = 0.33$, $p = 0.0093$). The difference in abundance patterns between brachiopods and filibranch, mainly epifaunal and semi-infaunal bivalves is lower in terms of Bray-Curtis similarity when compared to the comparison between brachiopods and eulamellibranchs, and R is also invariably lower. However, its significance varies among datasets. It is insignificant for the Lower Jurassic Foum Zidet Formation, the Bajocian formations of the High Atlas, and the Oxfordian formations of the

Swiss Jura. In contrast, abundance patterns of brachiopods and filibranch bivalves differ non-randomly in the Upper Triassic Fatra Formation (R = 0.386, p = 0.018), the Hybe Formation (R = 0.13, p = 0.04), the Kössen Formation (R = 0.17, p = 0.003), the Bajocian-Bathonian formations (R = 0.29, p < 0.0001), the Callovian-Oxfordian formations (R = 0.02, p = 0.01), and the Kimmeridgian-Berriasian formations of the Pieniny Klippen Belt (R = 0.23, p = 0.014). These results thus indicate that in addition to the difference between brachiopods and infaunal bivalves, environmental preferences of brachiopods differed also from preferences of epifaunal filibranch bivalves. Relationships between brachiopods, protobranchs and pseudolamellibranchs are mostly inconclusive owing to low species number in the two bivalve groups.

The observed differences in preferences of Late Triassic-Jurassic brachiopods and bivalves with respect to variations in terrigenous supply and wave-base level, and their segregated abundance patterns, are in accord with ecologic and physiologic observations on present-day rhynchonelliformean brachiopods, epifaunal bivalves, and infaunal bivalves. Bivalves in general are characterized by higher tolerance to high particle concentrations (Rhodes and Thompson, 1992, 1993) and have higher pumping rates than rhynchonelliformean brachiopods (LaBarbera, 1981b; Curry et al., 1989; James et al., 1992). They have thus better ability to cope with higher turbidity and sedimentation rates (Rhodes and Thayer, 1991), and should prefer environments with higher flow velocity than brachiopods. Preferences with respect to varying food supply are related to lower metabolic rates and thus lower food supply demands of brachiopods than of bivalves. Suspension-feeding bivalves differing in the gill type vary in feeding efficiency. In general, filibranch and pseudolamellibranch, mainly epifaunal bivalves have higher clearance rates than eulamellibranch, mainly infaunal bivalves. Filibranch and pseudolamellibranch bivalves are thus able to inhabit also food-poor environments similarly as brachiopods, but eulamellibranch bivalves seem to be limited in food-poor environments (Chapter 3). Therefore, even in environments without fluctuations in substrate consistency, it is expected that brachiopods will co-occur more commonly with epifaunal than with infaunal bivalves. The main argument of this study is that differences in distribution and abundance patterns between brachiopods and bivalves can be explained by variations in abiotic factors to a large degree, and that these differences are related not only to differences in substrate strategies, but also to differences in feeding strategies conditions. Although this study does address brachiopod niche expansion and truncation in time, the idea that the response of Late Triassic-Jurassic brachiopods to environmental variations is comparable to that of modern brachiopods implies that their niches remained relatively constant after the Jurassic.

The role of abiotic factors does not exclude possible effects of biotic interactions on distribution of brachiopods and bivalves, and the results of studies from the Lower Jurassic Foum Zidet Formation of Morocco indicate that differential abilities to compete for *space* and *food* might also play substantial role in their distribution. First, abundance of brachiopods correlates positively with abundance of microbial crusts, and abundance of the oyster *Nanogyra* correlates positively with percent cover of encrusters. Assuming that abundance of encrusters is positively correlated to intensity of live-live interactions, this implies that brachiopods preferred habitats with reduced grazing and/or reduced limitation of substrate space. This result is in accord with the expectation of escalation hypothesis (i.e., brachiopods are displaced by enemies – in this case by competitively inferior bivalves with high metabolic rates or other organisms with better abilities to compete for space) and with the actualistic observations about poor competitive abilities of brachiopods to compete for space on hard substrates (e.g., poor mobility and slow growth rates). Second, brachiopods formed dense shell beds in flow-limited habitats below storm wave base, implying that (1) they might deplete food and thus outcompete oysters characterized by reduced abilities to feed under flow-limited conditions, and/or (2) brachiopods developed specific adaptations to environments that were otherwise unfavourable for bivalves.

Therefore, differential environmental preferences of brachiopods and bivalves with respect to food supply and flow velocity, and possibly the effect of food depletion owing to the suspension-feeding activity of high-density populations of brachiopods in flow-limited environments, is not in accord with the simple hypotheses (1) that brachiopods were outcompeted on hard substrates by organisms with high-energy life styles, and (2) that brachiopods are adaptively anachronistic organisms. Rather, this suggests that brachiopods and bivalves evolved different life strategies, and that life strategies of brachiopods can be advantageous and thus competitively superior in some environments, especially those that are limited in food supply or flow velocity. It is suggested that the observed decline in community-level abundance of brachiopods since the Mesozoic can be mainly related to combined effects of (1) reduced availability of their preferred environments that vanished during the Cenozoic owing to the higher input nutrients into oceans (Bambach, 1993; Vermeij, 1995), and (2) co-related intensification of competition for space and other biological hazards in onshore environments that led to proliferation of organisms that maximized their energy expenditure such as bivalves.

14. References

Aberhan, M., 1992, Palökologie und zeitliche Verbreitung benthischer Faunengemeinschaften im Unterjura von Chile: Beringeria, v. 5, p. 3-174.

Aberhan, M., 1993, Faunal replacement in the Early Jurassic of northern Chile: implications for the evolution in Mesozoic benthic shelf ecosystems: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 103, p. 155-177.

Aberhan, M., 1994, Guild-structure and evolution of Mesozoic benthic shelf communities: Palaios, v. 9, p. 516-545.

Ackerman, J.D., and Nishizaki, M.T., 2004, The effect of velocity on the suspension-feeding and growth of the marine mussels *Mytilus trossulus* and *M. californianus*: implications for niche separation: Journal of Marine Systems, v. 49, p. 195-207.

Aerts, L.A.M., 1998, Sponge/coral interactions in Caribbean reefs: analysis of overgrowth patterns in relation to species indentity and cover: Marine Ecology Progress Series, v. 175, p. 241-249.

Ager, D.V., 1965, The adaptation of Mesozoic brachiopods to different environments: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 1, p. 143-172.

Ager, D.V., 1987, Why the rhynchonellid brachiopods survived and the spiriferids not: a suggestion: Palaeontology, v. 30, p. 853-857.

Aldinger, H., 1961, Die Schwammfazies im Weissen Jura Schwabens: Jahresberichte und Mitteilungen des oberrheinischen geologischen Vereines, N.F., v. 43, p. 99-103.

Alexander, R.R., 1977, Generic longevity of articulate brachiopods in relation to the mode of stabilization on the substrate: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 21, p. 209-226.

Alexander, R.R., 1986, Frequency of sublethal shell-breakage in articulate brachiopod assemblages through geologic time: in Racheboeuf, P.R., and Emig, C.C. (eds.), Les Brachiopodes fossiles et actuels: Biostratigraphie du Paléozoique, v. 4, p. 159-166.

Allenbach, R.P., 2001, Synsedimentary tectonics in an epicontinental sea: a new interpretation of the Oxfordian basins of northern Switzerland: Eclogae Geologicae Helvetiae, v. 94, p. 265-287.

Allenbach, R.P., 2002, The ups and downs of "tectonic quiescence"- recognizing differential subsidence in the epicontinental sea of the Oxfordian in the Swiss Jura Mountains: Sedimentary Geology, v. 150, p. 323-342.

Alméras, Y., and Hanzo, M., 1991, Les Rhynchonellidés du Calcaire à grypheés d`Hettange (Sinémurien-NE France): étude des peuplements et enregistrement des variations du paléonvironment: Palaeogeography Palaeoclimatology Palaeoecology, v. 86, p. 313-329.

Alméras, Y., and Sadki, D., 1992, Les Brachiopodes Bajociens inferieurs du Haut-Atlas Central au Sud de Midelt (Maroc): Paleontologie et phenomene de miniaturisation: Revue de Paléobiologie, v. 11, p. 167-195.

Alméras, Y., and Elmi, S., 1993, Palaeogeography, physiography, palaeoenvironments and brachiopod communities. Example of the Liassic brachiopods in the Western Tethys: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 100, p. 95-108.

Alméras, Y., Elmi, S., Mekahli, L., Ouali-Mehadjii, A., Sadki, D., and Tlili, M., 1994, Biostratigraphie des Brachiopodes du Jurassique moyen dans le domaine atlasique (Maroc, Algérie). Contraintes environnementales et relation avec l`évolution verticale des peuplements d`ammonites: Miscellanea del Servizio Geologico Nazionale, v. 5, p. 219-241.

Alroy, J., 2004, Are Sepkoski`s evolutionary faunas dynamically coherent?: Evolutionary Ecology Research, v. 6, p. 1-32.

Alunno-Bruscia, M., Bourget, E., and Fréchette, M., 2001, Shell allometry and length-mass-density relationship for *Mytilus edulis* in an experimental food-regulated situation: Marine Ecology Progress Series, v. 219, p. 177-188.

Aronson, R.B., Blake, D.B., and Oji, T., 1997, Retrograde community structure in the late Eocene of Antarctica: Geology, v. 25, p. 903-906.

Arboleya, M.L., Teixell, A., Charroud, M., and Julivert, M., 2004, A structural transect through the High and Middle Atlas of Morocco: Journal of African Earth Sciences, v. 39, p. 319-327.

Arp, G., Reimer, A., and Reitner, J., 2001, Photosynthesis-induced biofilm calcification and calcium concentrations in Phanerozoic oceans: Science, v. 292, p. 1701-1704.

Aubrecht, R., Mišík, M., and Sýkora, M., 1997, Jurassic synrift sedimentation on the Czorsztyn Swell of the Pieniny Klippen Belt in Western Slovakia: *in* Plašienka, D., Hók, J., Vozár, J., and Elečko, M. (eds.), Alpine evolution of the western Carpathians and related areas: Bratislava, Geological Survey of Slovak Republic, p. 53-64.

Aubrecht, R., Szulc, J., Michalík, J., Schlögl, J., and Wagreich, M., 2002, Middle Jurassic stromatactis mud-mound in the Pieniny Klippen Belt (Western Carpathians): Facies, v. 47, p. 113-126.

Bacon, G.S, MacDonald, B.A., and Ward, J.E., 1998, Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles. I. Feeding activity and selection: Journal of Experimental Marine Biology and Ecology: v. 219, p.105-125.

Bambach, R.K., 1993, Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystems: Paleobiology, v. 19, p. 372-397.

Bambach, R.K., 1999, Energetics in the global marine fauna: a connection between terrestrial diversification and change in the marine biosphere: Geobios, v. 32, p. 131-144.

Bambach, R.K., Bennington, J B., 1996, Do communities evolve? A major question in evolutionary paleoecology: in Jablonski, D., Erwin, J., and Lipps, J.H., eds., Evolutionary Paleobiology: Chicago and London, University of Chicago Press, p. 123-160.

Barczyk, W., 1979, Brachiopods from the Jurassic/Cretaceous bundary of Rogoźnik and Czorsztyn in the Pieniny Klippen Belt: Acta Geologica Polonica, v. 29, p. 207-214.

Barczyk, W., 1991, Succession of the Tithonian to Berriasian brachiopod faunas at Rogoźnik, Pieniny Klippen Belt: Acta Geologica Polonica, v. 41, p. 101-107.

Barnes, D.K.A., and Peck, L.S., 1997, An Antarctic shelf population of the deep-sea, Pacific brachiopod *Neorhynchia strebeli*: Journal of the Marine Biological Association of the United Kingdom, v. 77, p. 399-407.

Barnes, D.K.A., and Dick, M.H., 2000, Overgrowth competition between clades: implications for interpetation of the fossil record and overgrowth indices: Biological Bulletin, v. 199, p. 85-94.

Barnes, D.K.A., and Brockington, S., 2003, Zoobenthic biodiversity, biomass and abundance at Adelaide Island, Antarctica: Marine Ecology Progress Series, v. 249, p. 145-155.

Barthel, D., 1992, Do hexactinellids structure Antarctic sponge associations?: Ophelia, v. 36, p. 111-118.

Barthel, D., 1996, Fish eggs and pentacrinoids in Weddell Sea hexactinellids: further examples for the structuring role of sponges in Antarctic benthic ecosystems: Polar Biology, v. 17, p. 91-94.

Barthel, D., Tendal, O.S., and Thiel, H., 1996, A wandering population of the hexactinellid sponge *Pheronema carpenteri* on the continental slope off Morocco, Northwest Africa: Marine Ecology, v. 17, p. 603-616.

Barthel, K.W., and Schairer, G., 1978, Das Alter einiger Korallenriff- und Stotzenkalke des Oberjura entlang der Donau in Bayern: Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, v. 18, p. 11-27.

Bartolini, A., Pittet, B., Mattioli, E., and Hunziker, J.C., 2003, Shallow-platform palaeoenvironmental conditions recorded in deep-shelf sediments: C and O stable isotopes in Upper Jurassic sections of southern Germany (Oxfordian-Kimmeridgian): Sedimentary Geology, v. 160, p. 107-130.

Bartolini, A., Baumgartner, P.O., and Guex, J., 1999, Middle and Late Jurassic radiolarian palaeoecology versus carbon-isotope stratigraphy: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 145, p. 43-60.

Bartolini, A., and Cecca, F., 1999, 20 My hiatus in the Jurassic of Umbria-Marche Appennines (Italy): carbonate crisis due to eutrophication: Comptes Rendus de l'Academie des Sciences, Earth and Planetary Science, v. 329, p. 587-595.

Baumgartner, P.O., 1997, Age and genesis of Tethyan Jurassic radiolarites: Eclogae Geologicae Helvetiae, v. 80, p. 831-879.

Beauchamp, W., Allmendinger, R. W., Barazangi, M., Demnati, A., El Alji, M., and Dahmani, M., 1999, Inversion tectonics and the evolution of the High Atlas Mountains, Morocco, based on a geological-geophysical transect: Tectonics, v. 18, p. 263-184.

Behrensmeyer, A.K., Fürsich, F.T., Gastaldo, R.A., Kidwell, S.M., Kosnik, M.A., Kowalewski, M., Plotnick, R.E., Rogers, R.R., and Alroy, J., 2005, Are the most durable shelly taxa the most common in the marine fossil record: Paleobiology, v. 31, p. 607-623.

Benigni, C., Casati, P., and Radrizani, E C. P., 1982, Stratigrafia del giurasico dei Dintorni di Foza (Altopiano di Asiago): Rivista Italiana Palaeontologia, v. 88, p. 45-74.

Beninger, P.G., Decottignies, P., and Rince, Y., 2004, Localization of qualitative particle selection sites in the heterorhabdic filibranch Pecten maximus (Bivalvia:Pectinidae): Marine Ecology-Progress Series, v. 275, p. 163-173.

Bernecker, M., Weidlich, O., and Flügel, E., 1999, Response of Triassic reef coral communities to sea-level fluctuations, storms and sedimentation: evidence from a spectacular outcrop (Adnet, Austria): Facies, v. 40, p. 229-280.

Berra, F., and Jadoul, F., 1996, Norian serpulid and microbial bioconstructions: implications for the platform evolution in the Lombardy Basin (Southern Alps, Italy): Facies, v. 35, p. 143-162.

Bett, B.J., and Rice, A.L., 1992, The influence of hexactinellid sponge (*Pheronema carpenteri*) spicules on the patchy distribution of macrobenthos in the Porcupine Seabight (bathyal NE Atlantic): Ophelia, v. 36, p. 217-226.

Bijma, J., and Boekschoten, G.J., 1995, Recent bryozoan reefs and stromatolite development in brackish inland lakes, SW Netherlands: Senckenbergiana maritima, v. 17, p. 163-185.

Birkenmajer, K., 1977, Jurassic and Cretaceous lithostratigraphic units of the Pieniny Klippen Belt, Carpathians: Studia Geologica Polonica, v. 45, p. 1-158.

Birkenmajer, K., 1986, Stages and structural evolution of the Pieniny Klippen Belt Basin, Carpathians: Studia Geologica Polonica, v. 88, p. 7-32.

Blau, J., and Grün, B., 1996, Sedimentologische Beobachtungen im Rot-Schnöll-Bruch (Hettangium/Sinemurium) von Adnet (Österreich): Giessener geologische Schriften, v. 56, p. 95-106.

Blind, W., 1963, Die Ammoniten des Lias alpha aus Schwaben , von Fonsjoch und Breitenberg (Alpen) und ihre Entwicklung: Palaeontographica, v. 121A, p. 38-131.

Boehm, G., 1881, Die Fauna des Kelheimer Diceras-Kalkes. II. Bivalven: Palaeontographica, v. 28, p. 141-192.

Böhm, F., 2003, Lithostratigraphy of the Adnet Group (Lower to Middle Jurassic, Salzburg, Austria): Österreichische Akademie der Wissenschaften, Schriftenreihe Erdwissenschaftliche Kommission, v. 16, p. 231-268.

Böhm, F., Ebli, O., Krystyn, L., Lobitzer, H., Siblík, M., and Rakús, M., 1999, Fauna, stratigraphy and depositional environment of the Hettangian-Sinemurian (Lower Jurassic) of Adnet (Salzburg, Österreich): Abhandlungen der geologischen Bundesanstalt, v. 56, p. 143-271.

Bonuso, N., Newton, C.R., Brower, J.C., and Ivany, L.C., 2002, Does coordinated stasis yield taxonomic and ecologic stability?: Middle Devonian Hamilton Group of central New York: Geology, v. 30, p. 1055-1058.

Bottjer, D.J., and Jablonski, D., 1988, Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates: Palaios, v. 3, p. 540-560.

Boucot, A.J., 1983, Does evolution take place in an ecological vacuum?: Journal of Paleontology, v. 57, p. 1-30.

Boullier, A., 1976, Les Terébratulidés de l`Oxfordien du Jura et de la bordure sud du Bassin de Paris: Annales Scientigiques de l´Universite de Besançon, v. 27, p. 1-457.

Brachert, T.C., 1986, Kontinuierliche und diskontinuierliche Sedimentation im süddeutschen Oberjura (unteres Kimmeridge; Ludwag/Oberfranken, Nördliche Frankenalb): Facies, v. 15, p. 233-284.

Brachert, T.C., 1992, Sequence stratigraphy and paleo-oceanography of an open-marine mixed carbonate/siliciclastic succession (Late Jurassic, southern Germany): Facies, v. 27, p. 191-216.

Brett, C.E., 1998, Sequence stratigraphy, paleoecology, and evolution: biotic clues and responses to sea-level fluctuations: Palaios, v. 13, p. 241-262.

Brett, C.E., and Baird, G.C., 1995, Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin: *in* Erwin, D.H., and Anstey, R.L., eds., New approaches to speciation in the fossil record: Columbia University Press, New York, p. 285-315.

Brey, T., Peck, L.S., Gutt, J., Hain, S., and Arntz, W.E., 1995, Population dynamics of *Magellania fragilis*, a brachiopod dominating a mixed-bottom macrobenthic assemblage on the Antarctic shelf: Journal of the Marine Biological Association of the United Kingdom, v. 75, p. 857-869.

Brugger, F.-H., 1999, Ökomorphologische Variationen oberjurassischer Brachiopodenassoziationen Süddeutschlands: Berliner geowissenschaftliche Abhandlungen E, v. 29, 1-111.

Brunton, F.R., and Dixon, O.A., 1994, Siliceous sponge-microbe biotic associations and their recurrence through the Phanerozoic as reef mound constructors: Palaios, v. 9, p. 370-387.

Burne, R.V., and Moore, L.S., 1987, Microbialites: organosedimentary deposits of benthic microbial communities: Palaios, v. 2, p. 241-254.

Burchette, T.P., and Wright, V.P., 1992, Carbonate ramp depositional systems: Sedimentary Geology, v. 79, p. 3-57.

Burgess, P.M., 2001, Modeling carbonate sequence development without relative sea-level oscillations: Geology, v. 29, p. 1127-1130.

Bush, A.M., and Bambach, R.K., 2004. Did alpha diversity increase during the Phanerozoic? Lifting the veils of taphonomic, latitudinal, and environmental biases: Journal of Geology, v. 112, p. 625-642.

Butman, C.A., Frechette, M., Geyer, W.R., and Starczak, V.R., 1994, Flume experiments on food-supply to the blue mussel *Mytilus edulis* L as a function of boundary-layer flow: Limnology and Oceanography, v. 39, p. 1755-1768.

Buzas, M.A., and Culver, S.J., 1998, Assembly, disassembly, and balance in marine paleocommunities: Palaios, v. 13, p. 263-275.

Calef, C.E., and Bambach, R.K., 1973, Low nutrient levels in lower Paleozoic (Cambrian-Silurian) oceans: Geological Society of America Abstracts with Programs, v. 17, p. 529.

Cherns, L., and Wright, V.P., 2000, Missing molluscs as evidence of large-scale, early skeletal aragonite dissolution in a Silurian sea: Geology, v. 28, p. 791-794.

Chiantore, M., Cattaneo-Vietti, R., Albertelli, G., Misic, C., and Fabiano, M., 1998, Role of filtering and biodeposition by *Adamussium colbecki* in circulation of organic matter in Terra Nova Bay (Ross Sea, Antarctica): Journal of Marine Systems, v. 17, p. 411-424.

Childress, J.J., and Seibel, B.A., 1998, Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers: Journal of Experimental Biology, v. 201, p. 1223-1232.

Cirilli, S., Iannace, A., Jadoul, F., and Zamparelli, V., 1999, Microbial-serpulid buildups in the Norian-Rhaetian of the Western Mediterranean area: ecological response of shelf margin communities to stressed environments: Terra Nova, v. 11, p. 195-202.

Clarke, K.R., and Green, R.H., 1988, Statistical design and analysis for a “biological effects” study: Marine Ecology Progress Series, v. 46, p. 213-226.

Clarke, K.R., 1993, Non-parametric multivariate analyses of changes in community structure: Australian Journal of Ecology, v. 18, p. 117-143.

Clarke, K.R., and Warwick, R. M., 2001, Change in marine communities. An approach to statistical analysis and interpretation: PRIMER-E Ltd, Plymouth.

Climaco, A., Boni, M., Iannace, A., and Zamparelli, V., 1997, Platform margins, microbial/serpulid bioconstructions and slope-to-basin sediments in the Upper Triassic of the “Verbicaro Unit” (Lucania and Calabria, Southern Italy): Facies, v. 36, p. 37-56.

Cognie, B., Barille, L., Masse, G., and Beninger, P.G., 2003, Selection and processing of large suspended algae in the oyster Crassostrea gigas: Marine Ecology-Progress Series, v. 250, p. 145-152.

Colo, G., 1961, Contribution à l`étude du Jurassique du Moyen Atlas septentrional: Notes et Memoires du Service Geologique, v. 139, p. 1-226.

Conti, M.A., and Fischer, J.-C., 1982, La faune à gastropodes du Jurassique moyen de Case Canepine (Umbria, Italie), systématique, paléobiogéographie, paléoéecologie: Geologica Romana, v. 21, p. 125-183

Conti, M.A., and Monari, S., 1984, A middle Jurassic bivalve and gastropod fauna from Umbria (Central Italy): Geologica Romana, v. 23, p. 175-209.

Conti, M.A., and Szabó, J., 1987, Comparison of Bajocian gastropod faunas from the Bakony Mts. (Hungary) and Umbria (Italy): Annales Historico-naturales Musei Nationalis Hungarici, v. 79, p. 43-59.

Conti, M.A., and Monari, S., 1992, Thin-shelled bivalves from the Jurassic Rosso Ammonitico and Calcari a Posidonia Formations of the Umbrian-Marchean Apennine (Central Italy): Paleopelagos, v. 2, p. 193-213.

Courtillot, V., and Gaudemer, Y., 1996, Effects of mass extinctions on biodiversity: Nature, v. 381, p. 146-148.

Crame, J.A., 2002, Evolution of taxonomic diversity gradients in the marine realm: a comparison of Late Jurassic and Recent bivalve faunas: Paleobiology, v. 28, p. 184-207.

Curry, G.B., 1982, Ecology and population structure of the Recent brachiopod *Terebratulina* from Scotland: Palaeontology, v. 25, p. 227-246.

Curry, G., Ansell, A.D., James, M., and Peck, L., 1989, Physiological constraints on living and fossil brachiopods: Transactions of the Royal Society of Edinburgh: Earth Science, v. 80, p. 255-262.

Dame, R.F., 1996, Ecology of marine bivalves. An ecosystem approach: CRC Marine Science Series, Boca Raton, 254p.

De`ath, G., 1999, Principal curves: a new technique for indirect and direct gradient analysis: Ecology, v. 80, p. 2237-2253.

Delecat, S., Peckmann, J., and Reitner, J., 2001, Non-rigid cryptic sponges in oyster patch reefs (Lower Kimmeridgian, Langenberg/Oker, Germany): Facies, v. 45, p. 231-254.

Delecat, S., and Reitner, J., 2005, Sponge communities from the Lower Liassic of Adnet (Northern Calcareous Alps, Austria): Facies, v. 51, p. 399-418.

Dieni, I., and Middlemiss, F.A., 1981, Pygopid brachiopods from the Venetian Alps: Bolletino della Società Paleontologia Italiana, v. 20, p. 19-48.

Dietl, G.P., Alexander, R.R., and Bien, W.F., 2000, Escalation in Late Cretaceous-early Paleocene oysters (Gryphaeidae) from the Atlantic Coastal Plain: Paleobiology, v. 26, p. 215-237.

Digby, P.G.N., and Kempton, R.A., 1987, Population and community biology series: Multivariate analysis of ecological communities: Chapman and Hall, London, 206p.

DiMichele, W.A., Behrensmeyer, A.K., Olszewski, T.D., Labandeira, C.C., Pandolfi, J.M., Wing, L.S., and Bobe, R., 2004, Long-term stasis in ecological assemblages: evidence from the fossil record: Annual Reviews of Ecology and Systematics, v. 35, p. 285-322.

Dobretsov. S., Dahms, H.U., and Qian, P.Y., 2004, Antilarval and antimicrobial activity of waterborne metabolites of the sponge *Callyspongia (Euplacella) pulvinata*: evidence of allelopathy: Marine Ecology Progress Series, v. 271, p. 133-146.

Dobretsov. S., Dahms, H.U., Tsoi, M.Y, and Qian, P.Y., 2005, Chemical control of epibiosis by Hong Kong sponges: the effect of sponge extracts on micro- and macrofouling communities: Marine Ecology Progress Series, v. 297, p. 119-129.

Doherty, P.J., 1981, The contribution of dissolved amino acids to the nutrition of articulate brachiopods: New Zealand Journal of Zoology, v. 8, p. 183-188.

Doyle, P., and Whitham, A.G., 1991, Palaeoenvironments of the Nordenskjold Formation: an Antarctic Late Jurassic – Early Cretaceous black shale-tuff sequence: Special Publication, Geological Society, London, v. 58, p. 397-414.

Dresnay, R. du, 1963, Données stratigraphiques complémentaires sur le Jurassique moyen des synclinaux d`El Mers et de Skoura (Moyen Atlas, Maroc): Bulletin de la Societe Geologique de France, v. 5, p. 893-900.

Droser, M.L., Bottjer, D. J., and Sheehan, P. M., 1997, Evaluating the ecological architecture of major events in the Phanerozoic history of marine invertebrate life: Geology, v. 25, p. 167-170.

Dulai, A., 1990, The Lower Sinemurian (Jurassic) brachiopod fauna of the Lókút Hill (Bakony Mts., Hungary). Preliminary results: Annales Historico-Naturales Musei Nationalis Hungarici, v. 82, p. 25-37.

Dulai, A.,1993a, Hettangian (Early Jurassic) brachiopod fauna of the Bakony Mts. (Hungary): Fragmenta Mineralogica et Palaeontologica, v. 16, p. 27-50.

Dulai, A., 1993b, Hettangian (Early Jurassic) megafauna and paleogeography of the Bakony Mts. (Hungary): *in* Pálfy, J., and Vörös, A., eds., Mesozoic Brachiopods of Alpine Europe: Hungarian Geological Society, Budapest, p. 31-37.

Dulai, A., 2003, Taxonomic composition of Mediterranean Early Jurassic brachiopod faunas from Hungary: niche replacement and depth control: Fragmenta Palaeontogica Hungarica, v. 21, p. 43-50.

Dupraz, C., and Strasser, A., 1999, Microbialites and micro-encrusters in shallow coral bioherms (Middle to Late Oxfordian, Swiss Jura Mountains): Facies, v. 40, p. 101-130.

Dupraz, C., and Strasser, A., 2002, Nutritional modes in coral-microbialite reefs (Jurassic, Oxfordian, Switzerland): evolution of trophic structure as a response to environmental change: Palaios, v. 17, p. 449-471.

Dürr, S., and Wahl, M., 2004, Isolated and combined impacts of blue mussels (*Mytilus edulis*) and barnacles (*Balanus improvisus*) on structure and diversity of a fouling community: Journal of Experimental Marine Biology and Ecology, v. 306, p. 181-195.

Eckman, J.E., and Duggins, D.O., 1993, Effects of flow speed on growth of benthic suspension feeders: Biological Bulletin, v. 185, p. 28-41.

Erwin, D.H., 1998, The end and the beginning: recoveries from mass extinctions: Trends in Ecology and Evolution, v. 13, p. 344-349.

Erwin, D.H., 2001, Lessons from the past: biotic recoveries from mass extinctions: Proceedings of the National Academy of Sciences (Washington), v. 98, p. 5399-5403.

Evans, I., and Kendall, C. G. St. C. 1977, An interpretation of the depositional setting of some deep-water Jurassic carbonates of the Central High Atlas Mountains, Morocco: SEPM Special Publication, v. 25, p. 249-261.

Fagerstrom, J.A., West, R.R., Kershaw, S., and Cossey, P.J., 2000, Spatial competition among clonal organisms in extant and selected Paleozoic reef communities: Facies, v. 42, p. 1-24.

Finnegan, S., and Droser, M.L., 2005, Relative and absolute abundance of trilobites and rhynchonelliform brachiopods across the Lower/Middle Ordovician boundary, eastern Basin and Range: Paleobiology, v. 31, p. 480-502.

Flügel, E., and Steiger, T., 1981, An Upper Jurassic sponge-algal buildup from the Northern Frankenalb, west Germany: SEPM Special Publication, v. 30, p. 371-397.

Flügel, E., 2002, Triassic reef patterns: SEPM Special Publication, v. 72, p. 391-463.

Foote, M., 2000, Origination and extinction components of taxonomic diversity: general problems: *in* Erwin, D.H., and Wing, S.L., eds., Deep time. Paleobiology, Supplement to v. 26, p. 74-102.

Fözy, I., Kázmer, M., and Szente, I., 1994, A unique Lower Tithonian fauna in the Gerecse Mts, Hungary: Palaeopelagos, Special Publication, v. 1, p. 155-165.

Fréchette, M., and Bourget, E., 1985, Food-limited growth of *Mytilus edulis* in relation to the benthic boundary layer: Canadian Journal of Fisheries and Aquatic Sciences, v. 42, p. 1166-1170.

Fritz, G.K., 1958, Schwammstotzen, Tuberolithe und Schuttbreccien im Weissen Jura der Schwäbischen Alb: Arbeiten aus dem Geologisch-Paläontologischen Institut der Technischen Hochschule Stuttgart, N.F., v. 13, p. 1-118.

Fürsich, F.T., 1976, Fauna-substrate relationship in the Corallian of England and Normandy: Lethaia, v. 9, p. 343-356.

Fürsich, F.T., 1977, Corallian (Upper Jurassic) marine benthic associations from England and Normandy: Palaeontology, v. 20, p. 337-385.

Fürsich, F.T., and Hurst, J.M., 1974, Environmental factors determining the distribution of brachiopods: Palaeontology, v. 17, p. 879-900.

Fürsich, F.T., and Wendt, J., 1977, Biostratinomy and palaeoecology of the Cassian Formation (Triassic) of the Southern Alps: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 22, p. 257-323.

Fürsich, F.T., Oschmann, W., Jaitly, A.K., and Singh, I.B., 1991, Faunal response to transgressive-regressive cycles: example from the Jurassic of western India: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 85, p. 149-159.

Fürsich, F.T., Berndt, R., Scheuer, T., and Gahr, M., 2001, Comparative ecological analysis of Toarcian (Lower Jurassic) benthic faunas from southern France and east-central Spain. Lethaia, v. 34, p. 169-199.

Fürsich, F.T., Callomon, J.H., Pandey, D.K., and Jaitly, A.K., 2004a, Environments and faunal patterns in the Kachchh Rift Basin, western India, during the Jurassic: Rivista Italiana di Paleontologia e Stratigrafia, v. 110, p. 181-190.

Fürsich, F.T., Oschmann, W., Pandey, D.K., Jaitly, A.K., Singh, I.B., and Liu, C., 2004b, Palaeoecology of middle to lower Upper Jurassic macrofaunas of the Kachchh Basin, western India: an overview: Journal of the Palaeontological Society of India, v. 49, p. 1-26.

Futterer, E., 1982, Experiments on the distinction of wave and current influenced accumulations: *in* Einsele, G., and Seilacher, A., eds., Cyclic and event stratification: Springer-Verlag, Berlin, p. 175-179.

Gaetani, M., 1970, Faune hettangiane della parte orientale della provincial di Bergamo: Rivista Italiana di Paleontologia e Stratigrafia, v. 76, p. 355-442.

Gage, J.D., and Tyler, P.A., 1991, Deep-sea biology: a natural history of organisms at the deep-sea floor: Cambridge University Press, 504p.

Gahr, M.E., 2002, Palökologie des Makrobenthos aus dem Unter-Toarc SW-Europas: Beringeria, v. 31, p. 3-204.

Gahr, M., 2005, Response of Lower Toarcian (Lower Jurassic) macrobenthos of the Iberian Peninsula to sea level changes and mass extinction: Journal of Iberian Geology, v. 31, p. 197-215.

Galli, M.T., Jadoul, F., Bernasconi, S.M., and Weissert, H., 2005, Anomalies in global carbon cycling and extinction at the Triassic-Jurassic boundary: evidence from a marine C-isotope record: Palaeogeography Palaeoclimatology Palaeoecology, v. 216, p. 203-214.

Garcia, J.-P., and Dromart, G., 1997, The validity of two biostratigraphic approaches in sequence stratigraphic correlations: brachiopod zones amd marker-beds in the Jurassic: Sedimentary Geology, v. 114, p. 55-79.

Gardet, G., and Gérard, C., 1946, A l` étude paléontologique du Moyen-Atlas septentrional: Notes et Memoires, v. 64, p. 1-88.

Garrison, R.E., and Fisher, A.G., 1969, Deep-water limestones and radiolarites of the Alpine Jurassic: SEPM Special Publications, v. 14, p. 20-56.

Gaspard, D., 2003, Recent brachiopods collected during the "SEAMOUNT 1" cruise off Portugal and the Ibero-Moroccan Gulf (Northeastern Atlantic) in 1987: Geobios, v. 36, p. 285-304.

Gaździcki, A., 1974, Rhaetian microfacies, stratigraphy and facial development in the Tatra Mts: Acta Geologica Polonica, v. 24, p. 17-96.

Gaździcki, A., 1983, Foraminifers and biostratigraphy of Upper Triassic and Lower Jurassic of the Slovakian and Polish Carpathians: Palaeontologica Polonica, v. 44, p. 109-169.

Gaździcki, A., Michalík, J., Planderová, E., and Sýkora, M., 1979, An Upper Triassic - Lower Jurassic sequence in the Krížna nappe (West Tatra Mountains, West Carpathians, Czechoslovakia): Západné Karpaty, Geológia, v. 5, p. 119-148.

Genovese, S.J., and Witman, J.D., 1999, Interactive effects of flow speed and particle concentration on growth rates of an active suspension feeder: Limnology and Oceanography, v. 44, p. 1120-1131.

Gerdes, G., Kadagies, N., Kaselowsky, J., Lauer, A., and Scholz, J., 2005, Bryozoans and microbial communities of cool-temperate to subtropical latitudes – paleoecological implications. II. Diversity of microbial fouling on laminar shallow marine bryozoans of Japana and New Zealand: Facies, v. 50, p. 363-389.

Geyer, O.F., and Gwinner, M.P., 1979, Die Schwäbische Alb und ihr Vorland: Sammlung geologischer Führer 67, Gebrüder Borntraeger, Berlin-Stuttgart, 271p.

Gill, G.A., Santantonio, M., and Lathuilière, B., 2004, The depth of pelagic deposits in the Tethyan Jurassic and the use of corals: an example from the Apennines: Sedimentary Geology, v. 166, p. 311-334.

Gilinsky, N.L., and Bennington, J.B., 1994, Estimating numbers of whole individuals from collections of body parts: a taphonomic limitation of the paleontological record: Paleobiology, v. 20, p. 245-258.

Goetel, W., 1917, Die rhaetische Stufe und der unterste Lias der subtatrischen Zone in der Tatra: Bulletin International de l`Academie des Sciences de Cracovie, v. 1916, p. 1-222.

Golebiowski, R., and Braunstein, R. E., 1988, A Triassic/Jurassic Boundary Section in the Northern Calcareous Alps (Austria): Berichte der geologischen Bundesanstalt, v. 15, p. 39-46.

Golebiowski, R., 1989, Stratigraphie und Biofazies der Kössener Formation (Obertrias, Nördliche Kalkalpen): Unpublished PhD thesis, University of Vienna.

Golebiowski, R., 1990, The Alpine Kössen Formation, a key for European topmost Triassic correlations – a sequence and ecostratigraphic contribution to the Norian Rhaetian discussions: Albertiana, v. 8, p. 25-35.

Golebiowski, R., 1991, Becken und Riffe der alpinen Obertrias – Lithostratigraphie und Biofazies der Kössener Formation: Exkursionen im Jungpaläozoikum und Mesozoikum Österreichs, Österreichische Paläontologische Gesellschaft, Vienna, p. 79-119.

Golej, M., 2005, Rhaetian bivalves of the Hybe Formation: paleoecology and paleobiogeography: Unpublished Diploma Thesis, Comenius University, Bratislava, p. 1-84.

Golonka, J., and Krobicki, M., 2001, Upwelling regime in the Carpathian Tethys: a Jurassic-Cretaceous palaeogeographic and paleoclimatic perspective: Geological Quarterly, v. 45, p. 15-32.

Gotelli, N.J., and Graves, G.R., 1996, Null models in ecology: Smithsonian Institution Press, Washington, 368 p.

Gould, S.J., and Calloway, C.B., 1980, Clams and brachiopods - ships that pass in the night: Paleobiology, v. 6, p. 383-396.

Gradstein, F. M., Ogg, J. G., and Smith, A. G., 2004, A Geologic time scale 2004: Cambridge University Press, Cambridge, 589 p.

Grange, K.R., Singleton, R.J., Richardson, J.R., Hill, P.J., and Main, W. de L., 1981, Shallow rock-wall biological associations of some southern fiords of New Zealand: New Zealand Journal of Zoology, v. 8, p. 209-227.

Gray, J.S., Aschan, M., Carr, M.R., Clarke, R.K., Green, R.H., Pearson, T.H., Rosenberg, R., and Warwick, R.M., 1998, Analyssi of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment: Marine Ecology-Progress Series, v. 46, p. 151-165.

Grizzle, R.E., Langan, R., and Howell, W.H., 1992, Growth responses of suspension-feeding bivalve molluscs to changes in water flow: differences between siphonate and nonsiphonate taxa: Journal of Experimental Marine Biology and Ecology, v. 162, p. 213-228.

Guex, J., Bartolini, A., Atudorei, V., and Taylor, D., 2004, High-resolution ammonite and carbon isotope stratigraphy across the Triassic-Jurassic boundary at New York Canyon (Nevada): Earth and Planetary Science Letters, v. 225, p. 29-41.

Gutt, J., and Schickan, T., 1998, Epibiotic relationships in the Antarctic benthos: Antarctic Science, v. 10, p. 398-405.

Gutt, J., and Starmans, A., 1998, Structure and biodiversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions: Polar Biology, v. 20, p. 229-247.

Gygi, R.A., 1966, Über das zeitliche Verhältnis zwischen der transversarium-Zone in der Schweiz und der plicatilis-Zone in England (Unt. Malm, Jura): Eclogae Geologicae Helvetiae, v. 59, p. 935-942.

Gygi, R.A., 1969, Zur Stratigraphie der Oxford-Stufe (oberes Jura-System) der Nordschweiz und des süddeutschen Grenzgebietes: Beiträge geol. Karte Schweiz, v. 136, p. 1-123.

Gygi, R.A., 1977, Revision der Ammonitengattung *Gregoryceras* (Aspidoceratidae) aus dem Oxfordian (Oberer Jura) der Nordschweiz und von Süddeutschland. Taxonomie, Phylogenie, Stratigraphie: v. 70, p. 435-542.

Gygi, R.A., 1986, Eustatic sea level changes of the Oxfordian (Late Jurassic) and their effect documented in sediments and fossil assemblages of an epicontinental sea: Eclogae Geologicae Helveticae, v. 79, p. 455-491.

Gygi, R.A., 1990a, Die Paläogeographie im Oxfordium und frühesten Kimmeridgium in er Nordschweiz: Jahreshefte des geologischen Landesamtes Baden-Württemberg, v. 32, p. 207-222.

Gygi, R.A., 1990b, The Oxfordian ammonite succession near Liesberg BE and Péry BE, northern Switzerland: Eclogae Geologicae Helvetiae, v. 83, p. 177-199.

Gygi, R.A., 2000a, Integrated stratigraphy of the Oxfordian and Kimmeridgian (Late Jurassic) in northern Switzerland and adjacent southern Germany: Denkschriften der Schweizerischen Akademie der Naturwissenschaften, v. 104, p. 1-151.

Gygi, R.A., 2000b, Annotated index of lithostratigraphic units currently used in the Upper Jurassic of northern Switzerland: Eclogae Geologicae Helvetiae, v. 93, p. 125-146.

Gygi, R.A., Sadati, S.-M., and Zeiss, A., 1979, Neue Funde von Paraspidoceras (Ammonoidea) aus dem Oberen Jura von Mitteleuropa – Taxonomie, Ökologie, Stratigraphie: Eclogae Geologicae Helvetiae, v. 72, p. 897-952.

Gygi, R.A., and Persoz, F., 1986, Mineralostratigraphy, litho- and biostratigraphy combined in correlation of the Oxfordian (Late Jurassic) formations of the Swiss Jura range: Eclogae Geologicae Helveticae, v. 79, p. 385-454.

Gygi, R.A., and Persoz, F., 1987, The epicontinental sea of Swabia (southern Germany) in the Late Jurassic – factors controlling sedimentation: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 176, p. 49-65.

Gygi, R.A., Coe, A.L., and Vail, P.R., 1998, Sequence stratigraphy of the Oxfordian and Kimmeridgian Stages (Late Jurassic) in northern Switzerland: SEPM Special Publication, v. 60, p. 527-544.

Haas, J., Kovacs, S., Krystyn, L., and Lein, R., 1995, Significance of Late Permian - Triassic facies zones in terrane reconstruction in the Alpine – North Pannonian junction: Tectonophysics, v. 242, p. 19-40.

Hallam, A., 1960, A sedimentary and faunal study of the Blue Lias of Dorset and Glamorgan. Philosophical Transactions of the Royal Society, London B 243, p. 1-44.

Hallam, A., 1961, Brachiopod life assemblages from the Marlstone Rock-bed of Leicestershire: Palaeontology, v. 4, p. 653-659.

Hallam, A., 1975, Jurassic environments: Cambridge Earth Science Series, Cambridge University Press, Cambridge, 269p.

Hallam, A., 2002, How catastrophic was the end-Triassic mass extinction?: Lethaia, v. 35, p. 147-157.

Hallock, P., and Schlager, W., 1986, Nutrient excess and the demise of coral reefs and carbonate platforms: Palaios, v. 1, p. 389-398.

Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and analysis. Palaeontologia electronica 4, art.1, 9 pp. (http://palaeo-electronica.org/2001_1/past/issue1_01.htm).

Hansen, T.A., Kelley, P.H., and Haasl, D.M., 2004, Paleoecological patterns in molluscan extinctions and recoveries: comparison of the Cretaceous-Paleogene and Eoene-Oligocene extinctions in North America: Palaeogeography Palaeoclimatology Palaeoecology, v. 214, p. 233-242.

Harper, E.M., and Skelton, P.W., 1993, The Mesozoic Marine Revolution and epifaunal bivalves: Scripta Geologia, Special Issue, v. 2, p. 127-153.

Harries, P.J., Kauffman, E.G., and Hansen, T.A, 1996, Models for biotic survival following mass extinction: *in* Hart, M., ed., Biotic recovery from mass extinction events: Special Publication, Geological Society, London, v. 102, p. 41-60.

Harries, P.J., and Little, C.T.S., 1999, The early Toarcian (Early Jurassic) and the Cenomanian-Turonian (Late Cretaceous) mass extinctions: similarities and contrasts: Palaeogeography Palaeoclimatology Palaeoecology, v. 154, p. 39-66.

Hautmann, M., 2004a, Effect of end-Triassic CO_2 maximum on carbonate sedimentation and marine mass extinction: Facies, v. 50, p. 257-261.

Hautmann, M., 2004b, Early Mesozoic evolution of alivincular bivalve ligaments and its implications for the timing of the "Mesozoic marine revolution": Lethaia, v. 37, p. 165-172.

Hauptmann, M., 1990, Untersuchungen zur Mikrofazies, Stratigraphie und Paläogeographie jurassischer Karbonat-Gesteine im Atlas-System Zentral-Marokkos: Berliner Geowissenschaftliche Abhandlungen A, v. 119, p. 1-90.

Hawkins, A.J.S., Bayne, B.L., Bougrier, S., Héral, M., Iglesias, J.I.P., Navarro, E., Smith, R.F.M., and Urrutia, M.B., 1998, Some general relationships in comparing the feeding physiology of suspension-feeding bivalve molluscs: Journal of Experimental Marine Biology and Ecology, v. 219, p. 87-103.

Hawkins, A.J.S., Fang, J.G., Pascoe, P.L., Zhang, J.H., Zhang, X.L., and Zhu, M.Y., 2001, Modeling short-term responsive adjustments in particle clearance rate among bivalve suspension-feeders: separate unimodal effects of seston volume and composition in the scallop *Chlamys farreri*: Journal of Experimental Marine Biology and Ecology, v. 262, p. 61-73.

Hay, W.W., 1995, Paleoceanography of marine organic-carbon-rich sediments: AAPG Studies in Geology, v. 40, p. 21-59.

Hickman, C.S., 1984, Composition, structure, ecology, and evolution of six Cenozoic deep-water mollusk communities: Journal of Paleontology, v. 58, p. 1215-1234.

Hesselbo, S.P., Robinson, S.A., Surlyk, F., and Piasecki, S., 2002, Terrestrial and marine extinction at the Triassic-Jurassic boundary synchronized with major carbon-cycle perturbation: a link to initiation of massive volcanism?: Geology, v. 30, p. 251-254.

Hill, M.O., and Gauch, H.G., 1980, Detrended correspondence analysis: an improved ordination technique: Vegetatio, v. 42, p. 47-58.

Hill, M.S., 1998, Spongivory on Caribbean reefs releases corals from competition with sponges: Oecologia, v. 117, p. 143-150.

Hills, J.M., and Thomason, J.C., 2003, The "ghost of settlement past" determines mortality and fecundity in the barnacle, *Semibalanus balanoides*: Oikos, v. 101, p. 529-538.

Holland, S.M., 2005, The signatures of patches and gradients in ecological ordinations: Palaios, v. 20, p. 573-580.

Holland, S.M., Miller, A.I., Meyer, D.L., and Dattilo, B.F., 2001, The detection and importance of subtle biofacies within a single lithofacies: the Upper Ordovician Kope Formation of the Cincinnati, Ohio region: Palaios, v. 19, p. 205-217.

Holland, S.M., and Patzkowsky, M.E., 2004, Ecosystem structure and stability: Middle Upper Ordovician of Central Kentucky, USA: Palaios, v. 19, p. 316-331.

Holstein, B., 2004, Palynologische Untersuchungen der Kössener Schichten (Rhät, Alpine Obertrias): Jahrbuch der geologischen Bundesanstalt, v. 144, p. 261-365.

Hüssner, H., Goldberg, T., Hollstein, B., Petschick, R., Püttman, W., Roessler, J., Schubert, M., and Windt, A., 2000, Zyklostratigraphie und Biomarker in den oberen Kössener Schichten (Alpine Obertrias): Mitteilungen der Gesellschaft der Geologie- und Bergbaustudenten Österreich, v. 43, p. 65-66.

Iannace, A., and Zamparelli, V., 1996, The serpulid-microbialite bioconstructions of the "Scisti Ittiolici" basin of Giffoni Vallepiana (Upper Triassic, Southern Apennines): Palaeopelagos, v. 6, p. 45-62.

Iglesias, J.I.P., Urutia, M.B., Navarro, E., Alvarez Jorna, P., Larretxea, X., Bougrier, S., and Heral, M., 1996, Variability of feeding processes in the cockle *Cerastoderma edule* (L) in response to changes in seston concentration and composition: Journal of Experimental Marine Biology and Ecology, v. 197, p. 121-143.

Ivany, L.C., 1996, Coordinated stasis or coordinated turnover? Exploring intrinsic vs. extrinsic controls on pattern: Palaeogeography Palaeoclimatology Palaeoecology, v. 127, p. 239-256.

Jablonski, D., 2001, Lessons from the past: evolutionary impacts of mass extinctions: Proceedings of the National Academy of Sciences (Washington), v. 98, p. 5393-5398.

Jablonski, D., 2002, Survival without recovery after mass extinctions: Proceedings of the National Academy of Sciences (Washington), v. 99, p. 8139-8144.

Jablonski, D., and Bottjer, D.J., 1983, Soft-bottom epifaunal suspension-feeding assemblages in the late Cretaceous. Implications for the evolution of benthic paleocommunities: *in* Tevesz, M.J.S., and McCall, P.L., eds., Biotic interactions in recent and fossil benthic communities: Plenum Press, New York, p. 747-812.

Jablonski, D., and Raup, D.M., 1995, Selectivity of end-Cretaceous marine bivalve extinctions: Science, v. 268, p. 389-391.

Jablonski, D., Sepkoski, J.J., Jr., Bottjer, D.J., Sheehan, P.M., 1983, Onshore-offshore patterns in the evolution of Phanerozoic shelf communities: Science, v. 222, p. 1123-1125.

Jackson, J.B.C., 1983, Biological determinants of present and past sessile animal distributions: *in* Tevesz, M.J.S., and McCall, P.L., eds., Biotic interactions in recent and fossil benthic communities: Plenum Press, New York, p. 39-120.

Jackson, J.B., Goreau, T.F., and Hartman, W.D., 1971, Recent brachiopod-coralline sponge communities and their paleoecological significance: Science, v. 173, p. 623-625.

Jacobs, D.K., and Lindberg, D.R., 1998, Oxygen and evolutionary patterns in the sea: onshore/offshore trends and recent recruitment of deep-sea faunas: Proceedings of the National Academy of Sciences, v. 95, p. 9396-9401.

James, M.A., Ansell, A.D., Collins, M.J., Curry, G.B., Peck, L.S., and Rhodes, M.C., 1992, Biology of living brachiopods: Advances in Marine Biology, v. 28, p. 175-387.

Jenkyns, H.C., 1971, The genesis of condensed sequences in the Tethyan Jurassic: Lethaia, v. 4, p. 327-352.

Kamermans, P., 1993, Food limitation in cockles (*Cerastoderma edule* (L.)): influences of location on tidal flat and of nearby presence of mussel beds: Netherlands Journal of Sea Research, v. 31, p. 71-81.

Kauffman, E.G., and Harries, P.J., 1996, The importance of crisis progenitors in recovery from mass extinction: *in* Hart, M., ed., Biotic recovery from mass extinction events: Special Publications, Geological Society, London, v. 102, p. 15-39.

Kázmér, M., 1998, Pygopid brachiopods and Late Jurassic palaeorelief in the Gerecse Mts., Hungary: Földtani Közlöny, v. 128, p. 265-272.

Kelly, S.R.A., and Doyle, P., 1991, The bivalve Aulacomyella from the Early Tithonian (Late Jurassic) of Antarctica: Antarctic Science, v. 3, p. 97-107.

Kempe, S., Kazmierczak, J., Reimer, A., Landmann, G., and Reitner, J., 1996, Microbialites and hydrogeochemistry of the Crater Lake of Satonda – a status report: Göttinger Arbeiten zur Geologie und Paläontologie, Sonderband 2, p. 59-63.

Kenkel, N.C., and Orlóci, L., 1986, Applying metric and nonmetric multidimensional scaling to some ecological studies: some new results: Ecology, v. 67, p. 919-928.

Keupp, H., Koch, R., and Leinfelder, R., 1990, Steuerungsprozesse der Entwicklung von Oberjura-Spongiolithen Süddeutschlands: Kenntnisstand, Probleme und Perspektiven: Facies, v. 23, p. 141-174.

Kidwell, S.M., 1985, Palaeobiological and sedimentological implications of fossil concentrations: Nature, v. 318, p. 457-460.

Kidwell, S.M., 2005, Shell composition has no net impact on large-scale evolutionary patterns in mollusks: Science, v. 307, p. 914-917.

Kidwell, S.M., and Jablonski, D., 1983, Taphonomic feedback. Ecological consequences of shell accumulation: *in* Tevesz, M.J.S., and McCall, P.L., eds., Biotic interactions in recent and fossil benthic communities: Plenum Press, New York, p. 195-248.

Kiessling, W., and Baron-Szabo, R.C., 2004, Extinction and recovery patterns of scleractinian corals at the Cretaceous-Tertiary boundary: Palaeogeography Palaeoclimatology Palaeoecology, v. 214, p. 195-223.

Klitgaard, A.B., and Tendal, O.S., 2004, Distribution and species composition of mass occurrences of large-sized sponges in the northeast Atlantic: Progress in Oceanography, v. 61, p. 57-98.

Klug, S., Leinfelder, R.R., Nose, M., Schmid, D.U., and Werner, W., 2004, Paläoökologische Rekonstruktion sanddominierter Korallenhecken im Oberkimmeridgium von Saal a. d. Donau: 74th Annual Meeting of the Paläontologische Gesellschaft, Abstracts, p. 125-126.

Kment, K., 2000, Frühe liassischen Ammoniten aus der Gegend um Hinterriss im Karwendelgebirge (Tirol) und dem Mangfallgebirge bei Rottach-Egern (Bayern): Jahrbuch der geologischen Bundesanstalt, v. 142, p. 181-218.

Koch, R., Senowbari-Daryan, B., and Strauss, H., 1994, The Late Jurassic „Massenkalk Facies“ of southern Germany: calcareous sand piles rather than organic reefs: Facies, v. 31, p. 179-208.

Koch, R., and Senowbari-Daryan, B., 2000, Die fazielle Entwicklung im Steinbruch Blauberen/Altental (“Michelreibershalde”; Mittlere Schwäbische Alb, Blautal). Karbonatsandfazies des Malm epsilon und Riff-Rutschblöcke des Malm zeta 2: Jahresberichte und Mitteilungen des Oberrheinischen Geologischen Vereines, v. 82, p. 439-467.

Kochanová, M., 1979, Bivalvia and Gastropoda from the Vršatec Castle klippe: Západné Karpaty, Paleontológia, v. 4, p. 7-56.

Koslow, J.A., Gowlett-Holmes, K., Lowry, J.K., Poore, G.C.B., and Williams, A., 2001, Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling: Marine Ecology Progress Series, v. 213, p. 111-115.

Kosnik, M.A., 2005, Changes in Late Cretaceous-early Tertiary benthic marine assemblages: analyses from the North American coastal plain shallow shelf: Paleobiology, v. 31, p. 459-479.

Kostylev, V.E., Todd, B.J., Fader, G.B.J., Courtney, R.C., Cameron, G.D.M., and Pickrill, R.A., 2001, Benthic habitat mapping on the Scotian Shelf based on multibeam bathymetry, surficial geology and sea floor photographs: Marine Ecology Progress Series, v. 219, p. 121-137.

Kowalewski, M., and Demko, T., 1997, Trace fossils and population paleoecology: comparative analysis of size-frequency distribution: Lethaia, v. 29, p. 113-124.

Kowalewski, M., Simões, M.G., Carroll, M., and Rodland, D.L., 2002, Abundant brachiopods on a tropical, upwelling-influenced shelf (Southeast Brazilian Bight, South Atlantic): Palaios, v. 17, p. 277-286.

Kowalewski, M., Carroll, M., Casazza, L., Gupta, N., Hannisdal, B., Hendy, A., Krause, R.A., Jr., LaBarbera, M., Lazo, D.G., Messina, C., Puchalski, S., Rothfus, T.A., Sälgeback, J., Stempien, J., Terry, R.C., and Tomašových, A., 2003, Quantitative fidelity of brachiopod-mollusk assemblages from modern subtidal environments of San Juan Islands, USA: Journal of Taphonomy, v. 1, p. 43-65.

Kowalewski, M., Hoffmeister, A.P., Baumiller, T.K., and Bambach, R.K., 2005, Secondary evolutionary escalation between brachiopods and enemies of other prey: Science, v. 308, p. 1774-1777.

Krautter, M., Conway, K.W., Barrie, J.V., and Neuweiler, M., 2001, Discovery of a “living dinosaur”: globally unique modern hexactinellid sponge reefs off British Columbia, Canada: Facies, v. 44, p. 265-282.

Krebs, C.J., 1999, Ecological methodology: Addison Wesley Educational Publishers, Menlo Park, California, 620p.

Krobicki, M., 1993, Tithonian-Berriasian brachiopods in the Niedzica succession of the Pieniny Klippen Belt (Polish Carpathians): paleoecological and paleobiogeographical implications: in

Pálfy, J., and Vörös, A. (eds.), Mesozoic brachiopods of Alpine Europe: Hungarian Geological Society, Budapest, v. 69-77.

Krobicki, M., 1994, Stratigraphic significance and palaeoecology of the Tithonian-Berriasian brachiopods in the Pieniny Klippen Belt, Carpathians, Poland: Studia Geologica Polonica, v. 106, p. 89-156.

Krobicki, M., 1996, Neo-Cimmerian uplift of intraoceanic Czorsztyn pelagic swell (Pieniny Klippen Belt, Polish Carpathians) indicated by the changes of brachiopod assemblages: Georeserach Forum, v. 1-2, 255-264.

Kruskal, J.B., 1964, Multidimensional scaling by optimizng goodness of fit to a nonmetric hypothesis: Psychometrika, v. 29, p. 1-27.

Krystyn, L., Böhm, F., Kürschner, W., and Delecat, S., 2005, The Triassic-Jurassic boundary in the Northern Calcareous Alps: Abstract book of the 5th field workshop of IGCP project 458 (Budapest), p. A1-A39.

Kubanek, J., Whalen, K.E., Engel, S., Kelly, S.R., Henkel, T.P., Fenical, W., and Pawlik, J.R., 2002, Mulitple defensive roles for triterpene glycosides from two Caribbean sponges: Oecologia, v. 131, p. 125-136.

Kugler, C., 1987, Die Wildegg-Formation im Ostjuraund die Schilt-Formation im östlichen Helvetikum; ein Vergleich: Mitt. geol. Inst. ETH Univ. Zürich, v. 259, p. 1-209.

Kuss, J., 1983, Faziesentwicklung in proximalen Intraplatform-Becken: Sedimentation, Palökologie und Geochemie der Kössener Schichten (Ober-Trias, Nördliche Kalkalpen): Facies, v. 9, p. 61-172.

Kutek, J., and Wierzbowski, A., 1979, Lower to Middle Tithonian ammonite succession at Rogoźnik in the Pieniny Klippen Belt: Acta Geologica Polonica, v. 29, p. 195-205.

Kutek, J., and Wierzbowski, A., 1986, A new account on the Upper Jurassic stratigraphy and ammonites of the Czorsztyn succession, Pieniny Klippen Belt, Poland: Acta Geologica Polonica, v. 36, p. 289-316.

LaBarbera, M., 1977, Brachiopod orientation to water movement. 1. Theory, laboratory behavior, and field orientations: Paleobiology, v. 3, p. 270-287.

LaBarbera, M., 1981a, The ecology of Mesozoic *Gryphaea, Exogyra*, and *Ilymatogyra* (Bivalvia: Mollusca) in a modern ocean: Paleobiology, v. 7, p. 510-526.

LaBarbera, M., 1981b, Water flow patterns in and around three species of articulate brachiopods: Journal of Experimental Marine Biology and Ecology, v. 55, p. 185-206.

LaBarbera, M., 1984, Feeding currents and particle capture mechanisms in suspension-feeding animals: American Zoologist, v. 24, p. 71-84.

Lang, B., 1989, Die Schwamm-Biohermfazies der Nördlichen Frankenalb (Urspring; Oxford, Malm): Mikrofazies, Palökologie, Paläontologie: Facies, v. 20, p. 199-274.

Laville, E., Pique, A., Amrhar, M., and Charroud, M., 2004, A restatement of the Mesozoic Atlasic Rifting (Morocco): Journal of African Earth Sciences, v. 38, p. 145-153.

Laws, R.A., 1982, Late Triassic depositional environments and molluscan associations from west-central Nevada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 37, p. 131-148.

Leichter, J.J., and Witman, J.D., 1997, Water flow over subtidal rock walls: relation to distributions and growth rates of sessile suspension feeders in the Gulf of Maine: water flow and growth rates: Journal of Experimental Marine Biology and Ecology, v. 209, p. 293-307.

Leinfelder, R.R., 2001, Jurassic reef ecosystems: *in* Stanley, G.D., Jr., ed., The history and sedimentology of ancient reef systems: Kluwer Academic/Plenum Publishers, New York, p. 251-309.

Leinfelder, R.R., Nose, M., Schmid, D.U., and Werner, W., 1993, Microbial crusts of the Late Jurassic: composition, palaeoecological significance and importance in reef construction: Facies, v. 29, p. 38-42.

Leinfelder, R.R., Krautter, M., Laternser, R., Nose, M., Schmid, D.U., Schweigert, G., Werner, W., Keupp, H., Brugger, H., Herrmann, R., Rehfeld-Kiefer, U., Schroeder, J.H., Reinhold, C., Koch, R., Zeiss, A., Schweizer, V., Christmann, H., Menges, G., Luterbacher, H., 1994, The origin of Jurassic reefs: current research developments and results: Facies, v. 31, p. 1-56.

Leinfelder, R.R., Schmid, D.U., Nose, M., and Werner, W., 2002, Jurassic reef patterns – the expression of a changing globe: SEPM Special Publication, v. 72, p. 465-520.

Lenihan, H.S., Peterson, C.H., and Allen, J.M., 1996, Does flow speed also have a direct effect on growth of active suspension-feeders: an experimental test on oysters: Limnology and Oceanography, v. 41, p. 1359-1366.

Levin, L.A., 2003, Oxygen minimum zone benthos: adaptation and community response to hypoxia: Oceanography and Marine Biology: an Annual Review, v. 41, p. 1-45.

Lockwood, R., 2003, Abundance not linked to survival across the end-Cretaceous mass extinction: patterns in North American bivalves: Proceedings of the National Academy of Sciences (Washington), v. 100, p. 2478-2482.

Lockwood, R., 2004, The K/T event and infaunality: morphological and ecological patterns of extinction and recovery in veneroid bivalves: Paleobiology, v. 30, p. 507-521.

Lohse, D.P., 2002, Relative strengths of competition for space and food in a sessile filter feeder: Biological Bulletin, v. 203, p. 173-180.

Lopez Gappa, J.J., 1989, Overgrowth competition in an assemblage of encrusting bryozoans settled on artificial substrata: Marine Ecology Progress Series, v. 51, p. 121-130.

Löwner, R., Souhel, A., Chafiki, D., Canérot, J., and Klitzsch, E., 2002, Structural and sedimentologic relations between the High and the Middle Atlas of Morocco during the Jurassic time: Journal of African Earth Sciences, v. 34, p. 287-290.

Lucas, S.G., and Tanner, L.H., 2004, Late Triassic extinction events: Albertiana, v. 31, p. 31-40.

Mahon, A.R., Amsler, C.D., McClintock, J.B., Amsler, M.O., and Baker, B.J., 2003, Tissue-specific palatability and chemical defenses against macropredators and pathogens in the common articulate brachiopod *Liothyrella uva* from the Antarctic Peninsula: Journal of Experimental Marine Biology and Ecology, v. 290, p. 197-210.

Manceñido, M.O., 1993, First record of Jurassic nucleatid brachiopods from the southwest Pacific with comments on the global distribution of the group: Palaeogeography Palaeoclimatology Palaeoecology, v. 100, p. 189-207.

Manceñido, M.O., Owen, E.F., 2001. Post-paleozoic Rhynchonellida (Brachiopoda): classification and evolutionary background. In: Brunton, C.H.C., Cocks, L.R.M., Long, S.L. (Eds.), Brachiopods past and present. Taylor and Francis, London, 189-200.

Marin, A., and Belluga, M.D.L., 2005, Sponge coating decreases predation on the bivalve *Arca noae*: Journal of Molluscan Studies, v. 71, p. 1-6.

Martire, L., 1996, Stratigraphy, facies and synsedimentary tectonics in the Jurassic Rosso Ammonitico Veronese (Altopiano di Asiago, NE Italy): Facies, v. 35, p. 209-236.

Matyszkiewicz, J., 1997, Microfacies, sedimentation and some aspcts of diagenesis of Upper Jurassic sediments from the elevated part of the Northern peri-Tethyan Shelf: a comparative study on the Lochen area (Schwäbische Alb) and the Cracow area (Cracow-Wielun Upland, Polen): Berliner Geowissenschaftliche Abhandlungen, Reihe A, v. 21, p. 1-111.

Maughan, B.C., and Barnes, D.K.A., 2000, Seasonality of competition in early development of subtidal encrusting communities: Marine Ecology, v. 21, p. 205-220.

McCammon, H.M., 1969, The food of articulate brachiopods: Journal of Paleontology, v. 43, p. 976-985.

McCammon, H.M., and Reynolds, W.A., 1976, Experimental evidence for direct nutrient assimilation by the lophophore of articulate brachiopods: Marine Biology, v. 34, p. 41-51.

McClintock, J.B., Amsler, C.D., Baker, B.J., and van Soest, R.W.M., 2005, Ecology of Antarctic marine sponges: an overview: Integrative and Comparative Biology, v. 45, p. 359-368.

McCune, B., Grace, J.B., and Urban, D.L., 2002, Analysis of ecological communities: MjM Software Design, Gleneden Beach, 300 p.

McGhee, G. R., Jr., Sheehan, P.M., Bottjer, D. J., and Droser, M. L., 2004, Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic severities are decoupled: Palaeogeography Palaeoclimatology Palaeoecology, v. 211, p. 289-297.

McKinney, F., Lidgard, S., Sepkoski, J.J., Jr., and Taylor, P.D., 1998, Decoupled temporal patterns of evolution and ecology in two post-Paleozoic clades: Science, v. 281, p. 807-809.

McRoberts, C.A., and Newton, C.R., 1995, Selective extinction among end-Triassic European bivalves: Geology, v. 23, p. 102-104.

McRoberts, C.A., Newton, C.R., and Allasinaz, A., 1995, End-Triassic bivalve extinction: Lombardian Alps, Italy: Historical Biology, v. 9, p. 297-317.

McRoberts, C.A., Furrer, H., and Jones, D.S., 1997, Palaeoenvironmental interpretation of a Triassic-Jurassic boundary section from Western Austria based on palaeoecological and geochemical data: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 136, p. 79-95.

Mehdi, M., Neuweiler, F., and Wilmsen, M., 2003, Les formations du Lias inférieur du Haut Atlas central de Rich (Maroc): précisions lithostratigraphiques et étapes de l'évolution du bassin: Bull. Soc. Géol. France, v. 174, p. 227-242.

Meyer, R.K., and Schmidt-Kaler, H., 1989, Paläogeographischer Atlas des süddeutschen Oberjura (Malm): Geologische Jahrbuch, v. A115, p. 3-77.

Meyer, R.K., and Schmidt-Kaler, H., 1990, Paläogeographie und Schwammriffentwicklung des süddeutschen Malm – ein Überblick: Facies, v. 23, p. 175-184.

Michalík, J., 1973a, New information on the character of the Rhaetian at the locality near Hybe (northern slope of the Tatry Mts., Slovakia): Geologické Práce, Správy, v. 60, p. 197-212.

Michalík, J., 1973b, Paläogeographische Studie des Räts der Krížna-Decke des Strážov-Gebirges und einiger anliegender Gebiete: Geologický zborník – Geologica Carpathica, v. 24, p. 123-140.

Michalík, J., 1974, Zur Paläogeographie der Rhätische Stufe des weslichen Teiles der Krížna-Decke in der West-Karpaten: Geologický zborník – Geologica Carpathica, v. 25, p. 257-285.

Michalík, J., 1975, Genus *Rhaetina* Waagen, 1882 (Brachiopoda) in the uppermost Triassic of the West Carpathians: Geologický zborník – Geologica Carpathica, v. 26, p. 47-76.

Michalík, J., 1976, Two representatives of Strophomenida (Brachiopoda) in the uppermost Triassic of the West Carpathians: Geologický Zborník – Geologica Carpathica, v. 27, p. 79-96.

Michalík, J., 1977a, Paläogeographische Untersuchungen der Fatra-Schichten (Kossen - Formation) des nordlichen Teiles des Fatrikums in der Westkarpaten: Geologický zborník – Geologica Carpathica, v. 28, p. 71-94.

Michalík, J., 1977b, Systematics and ecology of *Zeilleria* Bayle and other brachiopods in the Uppermost Triassic of the West Carpathians: Geologický zborník – Geologica Carpathica, v. 28, p. 323-346.

Michalík, J., 1980, A paleoenvironmental and paleoecological analysis of the West Carpathian part of the Northern Tethyan nearshore region in the Latest Triassic time: Rivista Italiana di Paleontologia, v. 85, p. 1047-1064.

Michalík, J., 1982, Uppermost Triassic short-lived bioherm complexes in the Fatric, Western Carpathians: Facies, v. 6, p. 129-146.

Michalík, J., 1996, Functional morphology – paleoecology of pygopid brachiopods from the Western Carpathian Mesozoic: in Copper, P., and Jin, J. (eds.), Brachiopods: Proceedings of Third International Brachiopod Congress, A.A. Balkema, Rotterdam, p. 175-178.

Michalík, J., and Jendrejáková, O., 1978, Organism communities and biofacies of the Fatra Formation (Uppermost Triassic, Fatric) in the West Carpathians: Geologický zborník – Geologica Carpathica, v. 29, p. 113-137.

Michalík, J., Jendrejáková, O., Borza, K., 1979. Some new Foraminifera-species of the Fatra – Formation (Uppermost Triassic) in the West Carpathians. Geol. Zborn. – Geol. Carpath. 30, 61-91.

Michalík, J., Masaryk, P., Papšová, J., and Jendrejáková, O., 1988, Paleontology and biostratigraphy of the Upper Triassic formations in the Spiš- and Liptov Sub-Tatra regions: *in* Guide to the Paleontological conference of the Slovak Geological Society, Ruzbašská Miľava: Geological Institute of Dionyz Štúr, Bratislava, p. 5-21.

Michalík, J., Iordan, M., Radulović, V., Tchoumatchenco, P., and Vörös, A., 1991, Brachiopod faunas of the Triassic-Jurassic boundary interval in the Mediterranean Tethys: Geologica Carpathica, v. 42, p. 59-63.

Middleton, G.V., 1967, The orientation of concavo-convex particles deposited from experimental turbidity currents: Journal of Sedimentary Petrology, v. 37, p. 229-232.

Milhi, A., 1992, Stratigraphie, Fazies und Paläogeographie des Jura am Südrand des zetralen Hohen-Atlas (Marokko): Berliner Geowissenschaftliche Abhandlungen A, v. 144, p. 1-100.

Milhi, A., Ettaki, M., Chellai, E. H., and Hadri, M., 2002, Les formations lithostratigraphiques jurassiques du Haut-Atlas central (Maroc): corrélations et reconstitutions paléogéographiques: Revue de Paleobiologie, v. 21, p. 241-256.

Miller, A.I., 1988, Spatio-temporal transitions in Paleozoic Bivalvia: an analysis of North American fossil assemblages: Historical Biology, v. 1, p. 251-273.

Miller, A.I., 1998, Biotic transitions in global marine diversity: Science, v. 281, p. 1157-1160.

Miller, A.I., 2000, Conversations about Phanerozoic global diversity: *in* Erwin, D., and Wings, S.L., eds., Deep time: Paleobiology`s perspective: Paleobiology, Supplement to v. 26, p. 53-73.

Miller, A.I., and Connolly, S.R., 2001, Substrate affinities of higher taxa and the Ordovician Radiation: Paleobiology, v. 27, p. 768-778.

Minchin, P.R., 1987, An evaluation of the relative robustness of techniques for ecological ordination: Vegetatio, v. 69, p. 89-107.

Mišík, M., 1979, Sedimentological and microfacial study in the Jurassic of the Vršatec castle klippe (neptunic dykes, Oxfordian bioherm facies): Západné Karpaty, Geológia, v. 5, p. 7-56.

Mišík, M., 1993, The Czorsztyn submarine ridge (Jurassic-Lower Cretaceous, Pieniny Klippen Belt): an example of a pelagic swell: Mitteilungen der Österreichischen Geologischen Gesellschaft, v. 86, p. 133-140.

Mišík, M., 1997, The Slovak part of the Pieniny Klippen Belt after the pioneering works of D. Andrusov: Geologica Carpathica, v. 48, p. 209-220.

Mišík, M., Siblík, M., Sýkora, M., and Aubrecht, R., 1994, Jurassic brachiopods and sedimentological study of the Babiná klippe near Bohunice (Czorsztyn Unit, Pieniny Klippen Belt): Mineralia Slovaca, v. 26, p. 255-266.

Monbaron, M., 1981, Sédimentation, tectonique synsédimentaire at magmatisme basique: l`évolution paléogéographique et structurale de l`Atlas de Beni Mellal (Maroc) au cours du Mésozoïque; ses incidences sur la tectonique tertiaire: Eclogae Geologicae Helveticae, v. 74, p. 625-638.

Mostler, H., Scheuring, R., and Ulrichs, M., 1978, Zur Mega-, Mikrofauna und Mikroflora der Kössener Schichten (alpine Obertrias) vom Weissloferbach in Tirol unter besonderer Berücksichtigung der in der *suessi*- und *marshi*-Zone auftretenden Conodonten: Österreichische Akademie der Wissenschaften, Schriftenreihe Erdwissenschaftliche Kommission, v. 4, p. 141-174.

Morycowa, E., and Mišík, M., 2005, Upper Jurassic shallow-water scleractinian corals from the Pieniny Klippen Belt: Geologica Carpathica, v. 56, p. 415-432.

Mutti, M., and Hallock, P., 2003, Carbonate systems along nutrient and temperature gradients: some sedimentological and geochemical constraints: International Journal of Earth Sciences: v. 92, p. 465-475.

Navarro, J.M., Labarta, U., Fernandez-Reiriz, M.J., and Velasco, A., 2003, Feeding behavior and differential absorbtion of biochemical components by the infaunal bivalve *Mulinia edulis* and the epibenthic *Mytilus chilensis* in response to changes in food regimes: Journal of Experimental Marine Biology and Ecology, v. 287, p. 13-35.

Neuweiler, F., 1993, Development of Albian microbialites and microbialite reefs at marginal platform areas of the Vasco-Cantabrian Basin (Soba Reef Area, Cantabria, N. Spain): Facies, v. 29, p. 231-250.

Neuweiler, F., Mehdi, M., and Wilmsen, M., 2001, Facies of Liassic sponge mounds, Central High Atlas, Morocco: Facies, v. 44, p. 242-264.

Newton, C.A., Whalen, M.T., Thompson, J.B., Prins, N., and Delalla, D., 1987, Systematics and paleoecology of Norian (Late Triassic) bivalves from a tropical island arc: Wallowa Terrane, Oregon: Paleontological Society Memoir, v. 22, p. 1-83.

Nitzopoulos, G., 1974, Faunistisch-ökologische, stratigraphische und sedimentologische Untersuchungen am Schwammstotzen-Komplex bei Spielberg am Hahnenkamm (Ob. Oxfordien, Südliche Frankenalb): Stuttgarter Beiträge zur Naturkunde, Serie B, v. 16, p. 1-143.

Noble, J.P.A., Logan, A., and Webb, G.R., 1976, The Recent *Terebratulina* Community in the rocky subtidal zone of the Bay of Fundy, Canada: Lethaia, v. 9, p. 1-17.

Novack-Gottshall, P.M., and Miller, A.I., 2003a, Comparative taxonomic richness and abundance of Late Ordovician gastropods and bivalves in mollusc-rich strata of the Cincinnati Arch: Palaios, v. 18, p. 559-571.

Novack-Gottshall, P.M., and Miller, A.I., 2003b, Comparative geographic and environmental diversity dynamics of gastropods and bivalves during the Ordovician radiation: Paleobiology, v. 29, p. 576-604.

Nützel, A., and Erwin, D.H., 2004, Late Triassic (Late Norian) gastropods from the Wallowa Terrane (Idaho, USA): Paläontologische Zeitschrift, v. 78, p. 361-416.

Oji, T., 1996, Is predation intensity reduced with increasing depth? Evidence from the west Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic marine revolution: Paleobiology, v. 22, p. 339-351.

Okamura, B., and Partridge, J.C., 1999, Suspension feeding adaptations to extreme flow environments in a marine bryozoan: Biological Bulletin, v. 196, p. 205-215.

Okamura, B., Harmerlin J.-G., and Jackson, J.B.C., 2001, Refuges revisited. Enemies versus flow and feeding as determinants of sessile animal distribution and form: *in* Jackson, J.B.C., Lidgard, S., and McKinney, F.K. (eds.), Evolutionary patterns. Growth, form and tempo in the fossil record: University of Chicago Press, Chicago-London, p.61-93.

Olivier, N., Carpenter, C., Martin-Garin, B., Lathuilière, B., Gaillard, C., Ferry, S., Hantzpergue, P., and Geister, J., 2004a, Coral-microbialite reefs in pure carbonate versus mixed carbonate-siliciclastic depositional environments: the examples of the Pagny-sur-Meuse section (Upper Jurassic, northeastern France): Facies, v. 50, p. 229-255.

Olivier, N., Pittet, B., and Mattioli, E., 2004b, Palaeoenvironmental control on sponge-microbialite reefs and contemporaneous deep-shelf marl-limestone deposition (Late Oxfordian, southern Germany): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 212, p. 233-263.

Olszewski, T.D., and Patzkowsky, M., 2001, Measuring recurrence of marine biotic gradients: a case study from the Pennsylvanian-Permian Midcontinent: Palaios, v. 16, p. 444-460.

Oppel, A., 1863, Ueber das Vorkommen von jurassischen Posidonomyen-Gesteinen in den Alpen: Zeitschrift der deutschen geologischen Gesellschaft, v. 15, p. 188-217.

Oschmann, W., 1988, Upper Kimmeridgian and Portlandian marine macrobenthic associations from southern England and northern France: Facies, v. 18, p. 49-82.

Oschmann, W., 1994, Adaptive pathways of benthic organisms in marine oxygen-controlled environments: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 191, p. 393-444.

Ozanne, C.R., and Harries, P.J., 2002, Role of predation and parasitism in the extinction of the inoceramid bivalves: an evaluation: Lethaia, v. 35, p. 1-19.

Pálfy, J., 2003, Volcanism of the central Atlatic magmatic province as a potential driving force in the end-Triassic mass extinction: *in* Hames, W.E., McHone, J.G., Renne, and P.R., Ruppel C., eds., The Central Atlatic Magmatic Province: insights from fragments of Pangea: Geophysical Monograph Series, v. 136, p. 255-267.

Pálfy, J., Demény, A., Haas, J., Hetényi, M., Orchard, M.J., and Vetö, I., 2001, Carbon isotope anomaly and other geochemical changes at the Triassic-Jurassic boundary from a marine section in Hungary: Geology, v. 29, p. 1047-1050.

Palinska, K.A., Scholz, J., Sterflinger, K., Gerdes, G., and Bone, Y., 1999, Microbial mats associated with bryozoans (Coorong Lagoon, South Australia): Facies, v. 41, p. 1-14.

Palmer, T.J., and Wilson, M.A., 2004, Calcite precipitation and dissolution of biogenic aragonite in shallow Ordovician calcite seas: Lethaia, v. 37, p. 417-427.

Pandolfi, J.M., 1996, Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change: Paleobiology, v. 22, p. 152-176.

Patzkowsky, M.E., 1995, Gradient analysis of Middle Ordovician brachiopod biofacies: biostratigraphic, biogeographic, and macroevolutionary implications: Paleobiology, v. 10, p. 154-179.

Patzkowsky, M.E., and Holland, S.M., 1993, Biotic response to a Middle Ordovician paleoceanographic event in eastern North America: Geology, v. 21, p. 619-622.

Patzkowsky, M.E., Holland, S.M., 1997, Patterns of turnover in Middle and Upper Ordovician brachiopods of the eastern United States: a test of coordinated stasis: Paleobiology, v. 23, p. 420-443.

Paulsen, S., 1964, Aufbau und Petrographie des Riffkomplexes von Arnegg im höheren weissen Jura der Schwäbischen Alb (Württemberg): Arbeiten aus dem geologisch-Paläontologischen Institut der Technischen Hochschule Stuttgart, v. 42, p. 1-98.

Pawellek, T., and Aigner, T., 2003, Apparently homogenous "reef"-limestones built by high-frequency cycles: Upper Jurassic, SW-Germany: Sedimentary Geology, v. 160, p. 259-284.

Pearson, D.A.B., 1977, Rhaetian brachiopods of Europe: Neue Denkschriften des Naturhistorischen Museums in Wien, v. 1, p. 1-70.

Peck, L.S., 1996, Metabolism and feeding in the Antarctic brachiopod *Liothyrella uva*: a low energy lifestyle species with restricted metabolic scope: Proceedings of the Royal Society London, v. 263, p. 223-228.

Peck, L.S., Clarke, A., and Holmes, L.J., 1987, Summer metabolism and seasonal changes in biochemical composition of the Antarctic brachiopod *Liothyrella uva* (Broderip, 1833): Journal of Experimental Marine Biology and Ecology, v. 114, p. 85-97.

Peck, L.S., Curry, G.B., Ansell, A.D., and James, M., 1989, Temperature and starvation effects on the metabolism of the brachiopod *Terebratulina retusa* (L.): Historical Biology, v. 2, p. 101-110.

Peck, L.S., Barnes, D.K.A., and Willmott, J., 2005, Responses to extreme seasonality in food supply: diet plasticity in Antarctic brachiopods: Marine Biology, v. 147, p. 453-463.

Peters, S.E., 2004, Relative abundance of Sepkoski`s evolutionary faunas in Cambrian-Ordovician deep subtidal environments in North America: Paleobiology, v. 30, p. 543-560.

Peters, S.E., 2004, Relative abundance of Sepkoski`s evolutionary faunas in Cambrian-Ordovician deep subtidal environments in North America: Paleobiology, v. 30, p. 543-560.

Peterson, C.H., 1982, The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*: Ecological Monographs, v. 52, p. 437-475.

Pianka, E.R., 1994, Evolutionary Ecology: HarperCollins College Publishers, New York, 486p.

Pittet, B., Strasser, A., and Dupraz, C., 1995, Palaeoecology, palaeoclimatology and cyclostratigraphy of shallow-water carbonate-siliciclastic transitions in the Oxfordian of the Swiss Jura: IAS-16th Regional Meeting of Sedimentology, Field trip guide book, Publication ASF, Paris, p. 225-254.

Pittet, B., and Strasser, A., 1998, Long-distance correlations by sequence stratigraphy and cyclostratigraphy: examples and implications (Oxfordian from the Swiss Jura, Spain, and Normandy): Geologisches Rundschau, v. 86, p. 852-874.

Pittet, B., and Strasser, A., 1998b, Depositional sequences in deep-shelf environments formed through carbonate-mud import from the shallow platform (Late Oxfordian, German Swabian Alb and eastern Swiss Jura: Eclogae Geologicae Helvetiae, v. 91, p. 149-169.

Pittet, B., Strasser, A., Mattioli, E., 2000, Depositional sequences in deep-shelf environments: a response to sea-level changes and shallow-platform carbonate productivity (Oxfordian, Germany and Spain): Journal of Sedimentary Research, v. 70, p. 392-407.

Plöchinger, B., 1975, Das Juraprofil an der Zwölferhorn-Westflanke (Nördliche Osterhorngruppe, Salzburg): Verhandlungen der geologischen Bundesanstalt, v. 1975, p. 27-33.

Pörtner, H.O., Storch, D., and Heilmayer, O., 2005, Constraints and trade-offs in climate-dependent adaptation: energy budgets and growth in a latitudinal cline: Scientia Marina, v. 69 (Suppl. 2), p. 271-285.

Prantl, F., 1938, Erster Fund von Bryozoen in dem karpathischen Rhät: Zentralblatt für Mineralogie, Geologie und Paläontologie, Abhandlungen, v. 7, p. 262-264.

Rakús, M., 1992, Cephalopod fauna from Hybe Member of Kössen Fm. in Choč Nappe (West Carpathians): Západné Karpaty (Paleontológia), v. 17, p. 7-40.

Rakús, M., and Lobitzer, H., 1993. Early Liassic ammonites from the Steinplatte-Kammerköhralm area (Northern Calcareous Alps/Salzburg). Jahrbuch der geologischen Bundesanstalt, v. 136, p. 919-932.

Ramón, M., 1996, Relationships between the bivalves *Mytilus edulis* L. and *Cerastoderma edule* (L.) in a soft bottom environment: an example of interaction at small spatial scale: Journal of Experimental Marine Biology and Ecology, v. 204, p. 179-194.

Reháková, D., and Wierzbowski, A., 2005, Microfacies and stratigraphic position of the Upper Jurassic Rogoźa coquinas at Rogoźnik, Pieniny Klippen Belt, Carpathians: Volumina Jurassica, v. 3, p. 15-27.

Reitner, J., 1993, Modern cryptic microbialite/metazoan facies from Lizard Island (Great Barrier Reef, Australia) formation and concepts: Facies, v. 29, p. 3-40.

Reitner, J., and Keupp, H., 1991, The fossil record of the haplosclerid excavating sponge Aka de Laubenfels: in Reitner, J., and Keupp, H., eds., Fossil and recent sponges: Springer, Berlin, p. 102-120.

Richer de Forges, B., Koslow, J.A., and Poore, G.C.B., 2000, Diversity and endemism of the benthic seamount fauna in the southwest Pacific: Nature, v. 405, p. 944-947.

Richter, A.E., 2000, Geoführer Frankenjura. Geologische Sehenswürdigkeiten und Fossilfundstellen: Ammon Rey Verlag, Augsburg, 217p.

Reolid, M., 2005, Asociaciones de Braquiópodos del Oxfordiense medio-Kimmeridgiense inferior en la Zona Prebética (Sureste de España): Relación con las litofacies y el gradiente proximal-distal de la plataforma: Recista Española de Paleontología, v. 20, p. 21-36.

Reolid, M., Gaillard, C., Olóriz, F., and Rodríguez-Tovar, F.J., 2005, Microbial encrustations from the Middle Oxfordian-earliest Kimmeridgian lithofacies in the Prebetic Zone (Betic Cordillera, southern Spain): characterization, distribution and controlling factors: Facies, v. 50, p. 529-543.

Rhoads, D.C., 1974, Organism-sediment relations on the muddy seafloor: Oceanography and Marine Biology Annual Reviews, v. 12, p. 263-300.

Rhodes, M.C., and Thayer, C.W., 1991, Effects of turbidity on suspension-feeding: are brachiopods better than bivalves? : *in* MacKinnon, D.I., Lee, D.E., and Campbell, J.D., eds., Brachiopods through time: A. A. Balkema, Rotterdam, Brookfield, p. 191-196.

Rhodes, M.C., and Thompson, R.J., 1992, Clearance rate of the articulate brachiopod *Neothyris lenticularis* (Deshayes, 1839): Journal of Experimental Marine Biology and Ecology, v. 163, p. 77-89.

Rhodes, M.C., and Thompson, R.J., 1993, Comparative physiology of suspension-feeding in living brachiopods and bivalves: evolutionary implications: Paleobiology, v. 19, p. 322-334.

Rice, A.L., Thurston, M.H., and New, A.L., 1990, Dense aggregation of a hexactinellid sponge, *Pheronema carpenteri*, in the Porcupine Seabight (Northeast Atlantic Ocean) and possible causes: Progress in Oceanography, v. 24, p. 179-196.

Rice, M.A., and Stephens, G.C., 1987, Uptake and internal distribution of exogenously supplied amino acids in the Pacific oysters *Crassostrea gigas*: Aquaculture, v. 66, p. 19-31.

Richardson, J.R., 1981, Brachiopods and pedicles: Paleobiology, v. 7, p. 87-95.

Richardson, J.R., 1997, Ecology of articulated brachiopods: *in* Williams, A., Brunton, C.H.C., and Carlson, S.J., eds., Treatise on Invertebrate Paleontology, Part H. Brachiopoda Revised, Volume 1: Geological Society of America and University of Kansas Press, Boulder and Lawrence, p. 441-462.

Riding, R., 1997, Stromatolite decline: a brief reassessment: Facies, v. 36, p. 227-230.

Riding, R., 2000, Microbial carbonates: the geological record of calcified bacterial-algal mats and biofilms: Sedimentology, v. 47 (Supplement 1), p. 179-214.

Rodland, D.L., and Bottjer, D.J., 2001, Biotic recovery from the end-Permian mass extinction: behavior of the inarticulate brachiopod *Lingula* as a disaster taxon: Palaios, v. 16, p. 95-101.

Rodland, D.L., Kowalewski, M., Carroll, M., and Simões, M.G., 2004, Colonization of a "Lost World": Encrustation patterns in modern subtropical brachiopod assemblages: Palaios, v. 19, p. 381-395.

Rogers, A.D., 1994, The biology of seamounts: Advances in Marine Biology, v. 30, p. 305-350.

Rolley, J.-P., 1978, Carte geologique du Maroc Au 1/100.000 feuille Afourer (Haut Atlas central). Notice explicative: Notes et Memoires du Service Geologique du MAroc, v. 247, p. 5-103.

Roll, A., 1934, Form, Bau und Entstehung der Schwammstotzen im süddeutschen Malm: Paläontologische Zeitschrift, v. 16, p. 197-246.

Root, R.B., 1967, The niche exploitation pattern of the blue-gray gnatcatcher: Ecological Monographs, v. 37, p. 317-350.

Rosenberg, G.D., Hughes, W.W., and Tkachuck, R.D., 1988, Intermediary metabolism and shell growth in the brachiopod *Terebratalia transversa*: Lethaia, v. 21, p. 219-230.

Rosenzweig, M.L., and McCord, R.D., 1991, Incumbent replacement: evidence for long-term evolutionary progress: Paleobiology, v. 17, p. 202-213.

Rousselle, L., 1964, Discrimination de deux formes infraspécifiques chey une Rhynchonelle du Bathonien inferiéur de Bou-Rached (NE du Moyen-Atlas) marocain: Bulletin de la Societe Geologique de France, v. 6, p. 36-42.

Rousselle, L., 1965, Rhynchonellidae, Terebratulidae et Zeilleriidae du Dogger marocain (Moyen-Atlas septentrional, Hauts-Plateaux, Haut-Atlas): Notes et Memoires du Service Geologique, v. 187, p. 1-168.

Rousselle, L., 1967, Variation infraspécifique chey *Goniothyris buckmaniana* (Walker-Davidson), Térébratule du Dogger inférieur (Moyen-Atlas, Maroc): Bulletin de la Societe Geologique de France, v. 9, p. 43-48.

Rousselle, L., and Chavanon, S., 1981, Le genre *Cererithyris* (Brachiopodes, Terebratulidae) dans le Bajocien superieur et le Bathonien des Hauts-Plateaux du Maroc oriental: Compte Rendu Sommaire des Seances de la Societe Geologique de France, v. 3, p. 89-92.

Ruf, M., Link, E., Pross, J., and Aigner, T., 2005a, Integrated sequence stratigraphy: facies, stable isotope and palynofacies analysis in a deeper epicontinental carbonate ramp (Late Jurassic, SW Germany): Sedimentary Geology, v. 175, p. 391-414.

Ruf, M., Link, E., Pross, J., and Aigner, T., 2005b, A multi-proxy study of deeper-water carbonates (Upper Jurassic, southern Germany): combining sedimentology, chemostratigraphy and palynofacies: Facies, v. 51, p. 339-362.

Russ, G.R., 1982, Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks: Oecologia, v. 53, p. 12-19.

Salazar-Jiménez, A., Frey, R.W., and Howard, J.D., 1982, Concavity orientations of bivalve shells in estuarine and nearshore shelf sediments, Georgia: Journal of Sedimentary Petrology, v. 52, p. 565-586.

Sadki, D., 1992, Les variations de faciès et les discontinuités de sédimentation dans le Lias – Dogger du Haut-Atlas central (Maroc): chronologie, caractérisation, corrélations: Bulletin de la Societe Geologique de France, v. 163, p. 179-186.

Sadki, D., 1996, Le Haut-Atlas Central (Maroc): Stratigraphie et paléontologie du Lias supérieur et du Dogger inférieur. Dynamique du Bassin et des peuplements: Documents des Laboratoires de Géologie Lyon, v. 142, p. 1-245.

Sadki, D., and Alméras, Y., 1992, Les Brachiopodes Aaleno-Bajociens de la region de Rich (Haut-Atlas Central, Maroc): implications biostratigraphiques et paleoecologiques: Cahiers de l`Université Catholique de Lyon, v. 5, p. 93-105.

Sanders, D., 2003, Syndepositional dissolution of calcium carbonate in neritic carbonate environments: geological recognition, processes, potential significance: Journal of African Earth Sciences, v. 36, p. 99-134.

Sandy, M., 1995, Early Mesozoic (Late Triassic-Early Jurassic) Tethyan brachiopod biofacies: possible evolutionary intra-phylum niche replacement within the Brachiopoda: Paleobiology, v. 21, p. 479-495.

Sandy, M.R., 2001, Mesozoic articulated brachiopods from the Western Cordillera of North America: their significance for palaeogeographic and tectonic reconstruction, palaeobiogeography and palaeoecology: *in* Brunton, C.H.C., Cocks, L.R.M., Long, S.L., eds., Brachiopods past and present: Taylor and Francis, London, p. 394-410.

Sandy, M.R., 1993, and Stanley, G.D., Jr., 1993, Late Triassic brachiopods from the Luning Formation, Nevada, and their palaeobiogeographic significance: Palaeontology, v. 36, p. 439-480.

Santantonio, M., 1993, Facies associations and evolution of pelagic carbonate platform/basin systems: examples from the Italian Jurassic: Sedimentology, v. 40, p. 1039-1067.

Satterley, A.K., 1996, The interpretation of cyclic successions the Middle and Upper Triassic of the Northern Calcareous Alps: Earth-Science Reviews, v. 40, p. 181-207.

Savage, N.M., Manceñido, M.O., Owen, E.F., Carlson, S.J., Grant, R.E., Dagys, A.S., Sun, D.-L., 2002. Rhynchonellida. Treatise on invertebrate paleontology, part H, Brachiopoda revised, volume 4: Rhynchonelliformea (part), 1027-1377.

Scarponi, D., and Kowalewski, M., 2004, Stratigraphic paleoecology: bathymetric signatures and sequence overprint of mollusk associations from upper Quarternary sequences of the Po Plain, Italy: Geology, v. 32, p. 989-992.

Schädel, K., 1957, Ein geologisches Profil durch den Lochenstein bei Balingen: Jahrbuch den geologischen Landesamt Baden-Württemberg, v. 2, p. 175-178.

Schäfer, K., 1969, Vergleichs-Schaubilder zur Bestimmung des Allochemgehalts bioklastischer Karbonatgesteine: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, v. 1969, p. 173-184.

Schairer, G., and Sylla, J., 1996, Zum Alter der Kalke von Saal a. d. Donau: Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, v. 36, p. 73-80.

Schiaparelli, S., Albertelli, G., and Cattaneo-Vietti, R., 2003, The epibiotic assembly on the sponge *Haliclona dancoi* (Topsent, 1901) at Terra Nova Bay (Antarctica, Ross Sea): Polar Biology, v. 26, p. 342-347.

Schick, H., 2004a, Gliederung and Typusprofil der Lacunosamergel-Formation (Ober-Jura, Schwäbische Alb): Stuttgarter Beiträge zur Naturkunde, Serie B, v. 346, p. 1-25.

Schick, H., 2004b, Bio- and lithostratigraphic study on the Lower Kimmeridgian of the Swabian and Franconian Alb (Germany): Rivista Italiana di Paleontologia e Stratigrafia, v. 110, p. 279-288.

Schlosser, M., 1881a, Die Fauna des Kelheimer Diceras-Kalkes. I. Vertebrata, Crustacea, Cephalopoda, und Gastropoda: Palaeontographica, v. 28, p. 1-40.

Schlosser, M., 1881b, Die Brachiopoden des Kelheimer Diceras-Kalkes.: Palaeontographica, v. 28, p. 193-212.

Schmid, D., 1996, Marine Mikrobolithe und Mikroinkrustierer aus dem Oberjura: Profil, v. 9, p. 101-251.

Schmid, D.U., Leinfelder, R.R., and Nose, M., 2001, Growth dynamics and ecology of Upper Jurassic mounds, with comparisons to mid-Paleozoic mounds: Sedimentary Geology, v. 145, p. 343-376.

Schmid, D.U., Leinfelder, R.R., and Schweigert, G., 2005, Stratigraphy and palaeoenvironments of the Upper Jurassic of Southern Germany – a review: Zitteliana, v. B26, p. 31-41.

Schmidt-Kaler, H., 1991, Wanderungen in die Erdgeschichte (III). Vom neuen Fränkischen Seenland zum Hahnenkamm und Hesselberg: Verlag Friedrich Pfeil, München, 80p.

Scholz, J., and Hillmer, G., 1995, Reef-bryozoans and bryozoan-microreefs: control factor evidence from the Philippines and other regions: Facies, v. 32, p. 109-144.

Schubert, J.K., and Bottjer, D.J., 1992, Early Triassic stromatolites as post-mass extinction disaster forms: Geology, v. 20, p. 883-886.

Schubert, J.K., and Bottjer, D.J., 1995, Aftermath of the Permian-Triassic mass extinction event: paleoecology of Lower Triassic carbonates in the western USA: Palaeogeography Palaeoclimatology Palaeoecology, v. 116, p. 1-39.

Selg, M., and Wagenplast, P., 1990, Beckenarchitektur im süddeutschen Weissen Jura und die Bildung der Schwammriffe: Jahreshefte des geologischen Landesamtes Baden-Württemberg, v. 32, p. 171-206.

Sepkoski, J.J., Jr., 1979, A kinetic model of Phanerozoic taxonomic diversity. II. Early Phanerozoic families and multiple equilibria: Paleobiology, v. 5, p. 222-251.

Sepkoski, J.J., Jr., 1981, A factor analytic description of the Phanerozoic marine fossil record: Paleobiology, v. 7, p. 36-53.

Sepkoski, J.J., Jr., 1984, A kinetic model of Phanerozoic taxonomic diversity. III. Post-paleozoic families and mass extinctions: Paleobiology, v. 10, p. 246-267.

Sepkoski, J.J., Jr., 1991, A model of onshore-offshore change in faunal diversity: Paleobiology, v. 17, p. 58-77.

Sepkoski, J.J., Jr., 1996, Competition in macroevolution: *in* Jablonski, D., Erwin, J., and Lipps, J.H., eds., Evolutionary Paleobiology: Chicago and London, University of Chicago Press, p. 211-255.

Sepkoski, J.J., Jr., and Sheehan, P.M., 1983, Diversification, faunal change, and community replacement during the Ordovician radiations: *in* Tevesz, M. J. S, and McCall, P.L., eds., Biotic interactions in recent and fossil benthic communities: Plenum Press, New York, p. 673-717.

Sepkoski, J.J., Jr., and Miller, A., 1985, Evolutionary faunas and the distribution of Paleozoic benthic communities in space and time: *in* Valentine, J.W., ed., Phanerozoic diversity patterns: profiles in macroevolution: Princeton, Princeton University Press, p. 153-190.

Sepkoski, J.J., Jr., and Kendrick, D.C., 1993, Numerical experiments with model monophyletic and paraphyletic units: Paleobiology, v. 19, p. 168-184.

Sepkoski, J.J., Jr., McKinney, F.K., and Lidgard, S., 2000, Competitive displacement among post-Paleozoic cyclostome and cheilostome bryozoans: Paleobiology, v. 26, p. 7-18.

Sheehan, P.M., 1996, A new look at Ecologic Evolutionary Units (EEUs): Palaeogeography Palaeoclimatology Palaeoecology, v. 127, p. 21-32.

Shi, G.R., 1993, Multivariate data analysis in palaeoecology and palaeobiogeography – a review: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 105, p. 199-234.

Siblík, M., 1966, The brachiopods of the Kostelec-Klippe: Geologické Práce, Zprávy, v. 38, p. 137-157.

Siblík, M., 1967, The brachiopods of the Norian locality Drnava (southern Slovakia): Geologické Práce, Zprávy, v. 43, p. 81-97 (in Czech, with English Abstr.).

Siblík, M., 1979, Brachiopods of the Vršatec Castle Klippen (Bajocian-?Berriasian) near Ilava (Slovakia): Západné Karpaty, Paleontológia, v. 4, p. 35-64.

Siblík, M., 1993a, Review of the Early Liassic Brachiopods of the Northern Calcareous Alps: *in* J. Pálfy, and A. Vörös, eds., Mesozoic Brachiopods of Alpine Europe: Hungarian Geological Society, Budapest, p. 127-132.

Siblík, M., 1993b, Lower Liassic brachiopods from Steinplatte-Kammerköhralm Area near Waidring (Northern Calcareous Alps, Salzburg): Jahrbuch der geologischen Bundesanstalt, v. 136, p. 965-982.

Siblík, M., 1998, A contribution to the brachiopod fauna of the “Oberrhätkalk” (Northern Calcareous Alps, Tyrol-Salzburg): Jahrbuch der geologischen Bundesanstalt, v. 141, p. 73-95.

Siblík, M., 1999, New data on the Hettangian brachiopod fauna of the Northern Calcareous Alps (Austria, Bavaria): Abhandlungen der geologischen Bundesanstalt, v. 56, p. 419-438.

Simberloff, D., and Dayan, T., 1991, The guild concept and the structure of ecological communities: Annual Reviews of Ecology and Systematics, v. 22, p. 115-143.

Smith, A.B., Gale, A.S., and Monks, N.E.A., 2001, Sea-level changes and rock-record bias in the Cretaceous: a problem for extinction and biodiversity studies: Paleobiology, v. 27, p. 241-253.

Snelgrove, P.V.R., and Butman, C.A., 1994, Animal-sediment relationships revisited: cause versus effect: Oceanography and Marine Biology: an Annual Review, v. 32, p. 111-177.

Souhel, A., 1996, Le Mesozoique dans le Haut-Atlas de Beni-Mellal (Maroc): Strata, v. 27, p. 1-249.

Stanley, R.G., 1981, Middle Jurassic shoaling of the Central High Atlas sea near Rich, Morocco: Journal of Sedimentary Petrology, v. 51, p. 895-907.

Stanley, G.D., Jr., González-León, C., Sandy, M.R., Senowbari-Daryan, B., Doyle, P., Tamura, M., and Erwin, D.H., 1994, Upper Triassic invertebrates from the Antimonio Formation, Sonora, Mexico: Journal of Paleontology Memoir, v. 36, p. 1-33.

Stanley, S.M., 1968, Post-paleozoic adaptive radiation of infaunal bivalve molluscs – a consequence of mantle fusion and siphon formation: Journal of Paleontology, v. 42, p. 214-229.

Stanton, R.J., Jr., and Flügel, E., 1989, Problems with reef models: the Late Triassic Steinplatte "reef" (Northern Calcareous Alps, Salzburg, Tyrol, Austria): Facies, v. 20, p. 1-138.

Stanton, R.J., Jr., and Flügel, E., 1995, An accretionary distally steepened ramp at an intrashelf basin margin: an alterantive explanation for the Upper Triassic Steinplatte „reef" (Northern Calcareous Alps, Austria): Sedimentary Geology, v. 95, p. 269-286.

Starmans, A., Gutt, J., and Arntz, W.E., 1999, Mega-benthic communities in Arctic and Antarctic shelf areas: Marine Biology, v. 135, p. 269-280.

Steele-Petrović, H.M., 1976, Brachiopod food and feeding processes: Palaeontology, v. 19, p. 417-436.

Steele-Petrović, H.M., 1979, The physiological differences between articulate brachiopods and filter-feeding bivalves as a factor in the evolution of marine level-bottom communities: Palaeontology, v. 22, p. 101-134.

Stewart, I.R., 1981, Population structure of articulate brachiopod species from soft and hard substrates: New Zealand Journal of Zoology, v. 8, p. 197-207.

Stillman, R.A., McGrotry, S., Goss-Custard, J.D., and West, A.D., 2000, Predicting mussel population density and age structure: the relationship between model complexity and predictive power: Marine Ecology Progress Series, v. 208, p. 131-145.

Sturani, C., 1967, Reflexions sur les faciès lumachelliques du Dogger Mésogéen ("Lumachelle á *Posidonia alpina*" Auctt.): Bolletino della Societa Geologica Italiana, v. 86, p. 445-467.

Sturani, C., 1971, Ammonites and stratigraphy of the "*Posidonia alpina*" beds of the Venetian Alps: Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova, v. 28, p. 1-190.

Suess, E., and Mojsisovics, E., 1868, Studien über Gliederung der Trias- und Jurabildungen in den östlichen Alpen. II. Die Gebirgsgruppe des Osterhorns: Jahrbuch der kaiserlich-königlichen geologischen Reichsanstanstalt, v. 18, p. 167-200.

Szente, I., 1995a, Bivalves from a Middle Jurassic submarine high (Bajocian, Som Hill, Bakony Mts., Hungary): Hantkeniana, v. 1, p. 59-66.

Szente, I., 1995b, Bivalvia from the Bathonian (Middle Jurassic) of the Mecsek Mts, Hungary: Annales Universitatis Scientiarum Budapestinensis, Sectio Geologica, 30, p. 93-109.

Talman, S.G., and Keough, M.J., 2001, Impact of an exotic clam, *Corbula gibba*, on the commercial scallop *Pecten fumatus* in Port Phillip Bay, south-east Australia: evidence of resource-restricted growth in a subtidal environment: Marine Ecology Progress Series, v. 221, p. 135-143.

Taylor, P.D., and Michalík, J., 1991, Cyclostome bryozoans from the late Triassic (Rhaetian) of the West Carpathians, Czechoslovakia: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 182, p. 285-302.

Tchorszhevsky, E.S., and Radulović, V., 1984, New data of Middle Jurassic terebratulids (Brachiopoda) of the Carpathians (USSR) and Carpatho-Balkanides (Yugoslavia): Annales Géologiques de la Péninsule Balkanique, v. 48 p. 129-184.

Tchoumatchenco, P., 1972, Thanatocoenoses and biotopes of Lower Jurassic brachiopods in central and western Bulgaria: Palaeogeography Palaeoclimatology Palaeoecology, v. 12, p. 227-250.

Tchoumatchenco, P.V., 1993. The horizontal distribution of brachiopods during the *Zeilleria quadrifida* Zone (Late Carixian-Early Domerian, Early Jurassic) in Bulgaria: *in* J. Pálfy, and A. Vörös, eds., Mesozoic Brachiopods of Alpine Europe: Hungarian Geological Society, Budapest, p. 143-150.

ter Braak, C.J.F., and Prentice, I.C., 1988, A theory of gradient analysis: Advances in Ecological Research, v. 18, p. 271-313.

Termier, H., 1936, Etudes géologiques sur le Maroc central et le Moyen Atlas septentrional. Tome II: les terrains post-triasiques. Notes et Memoires du Service Geologique, v. 33, p. 743-1082.

Thayer, C.W., 1975, Morphologic adaptations of benthic invertebrates to soft substrata: Journal of Marine Research, v. 33, p. 177-189.

Thayer, C.W., 1977, Recruitment, growth and mortality of a living articulate brachiopod, with implications for the interpretation of survivorship curves: Paleobiology, v. 3, p. 98-109.

Thayer, C.W., 1979, Biological bulldozing and the evolution of marine benthic communities: Science, v. 203, p. 458-461.

Thayer, C.W., 1983, Sediment-mediated biological disturbance and the evolution of marine benthos: *in* Tevesz, M.J.S., and McCall, P.L., eds., Biotic interactions in recent and fossil benthic communities: Plenum Press, New York, p. 479-625.

Thayer, C.W., 1985, Brachiopods versus mussels: competition, predation, and palatability: Science, v. 228, p. 1527-1528.

Thayer, C.W., 1986, Are brachiopods better than bivalves? Mechanisms of turbidity tolerance and their interaction with feeding in articulated brachiopods: Paleobiology, v. 12, p. 161-174.

Thayer, C.W., and Allmon, R.A., 1990, Unpalatable thecideid brachiopods from Palau: ecological and evolutionary implications: in MacKinnon, D.I., Lee, D.E., and Campbell, J.D. (eds.), Brachiopods through time: Balkema, Rotterdam, p. 253-260.

Tkachuck, R.D., Rosenberg, G.D., and Hughes, W.W., 1989, Utilization of free amino acids by mantle tissue of the brachiopod *Terebratalia transversa* and the bivalve mollusc *Chlamys hastata*: Comparative Biochemistry and Physiology, v. 92B, p. 747-750.

Tomašových, A., 2004a, Microfacies and depositional environment of an Upper Triassic intra-platform carbonate basin: the Fatric Unit of the West Carpathians (Slovakia): Facies, v. 50, p. 77-105.

Tomašových, A., 2004b, Effect of extrinsic factors on biofabric and brachiopod alteration in a shallow intraplatform carbonate setting (Upper Triassic, West Carpathians): Palaios, v. 19, p. 349-371.

Tomašových, A., 2006a, Brachiopod and bivalve ecology in Late Triassic (Alps, Austria): onshore-offshore replacements caused by variations in sediment and nutrient supply: Palaios, v. 21 [in press].

Tomašových, A., 2006b. A new Early Jurassic rhynchonellid brachiopod from the western Tethys and implications for systematics of rhynchonellids from the Triassic – Jurassic boundary: Journal of Paleontology, v. 80, p. 212-228.

Tomašových, A., Fürsich, F.T., and Wilmsen, M., 2006, Preservation of autochthonous shell beds by positive feedback between increased hardpart-input rates and increased sedimentation rates: Journal of Geology, in press.

Tomašových, A., and Michalík, J., 2000, Rhaetian/Hettangian passage beds in the carbonate development in the Krížna Nappe (central Western Carpathians, Slovakia): Slovak Geological Magazine, v. 6, p. 241-249.

Tomašových, A., and Farkaš, J., 2005, Cathodoluminescence of Late Triassic terebratulid brachiopods: implications for growth patterns: Palaeogeography Palaeoclimatology Palaeoecology, v. 216, p. 215-233.

Tunnicliffe, V., and Wilson, K., 1988, Brachiopod populations: distribution in fjords of British Columbia (Canada) and tolerance of low oxygen concentrations: Marine Ecology-Progress Series, v. 47, p. 117-128.

Turnšek, D., Dolenec, T., Siblík, M., Ogorelec, B., Ebli, O., and Lobitzer, H., 1999, Contributions to the Fauna (Corals, Brachiopods) and Stable Isotopes of the Late Triassic Steinplatte Reef/Basin-Complex, Northern Calcareous Alps, Austria: Abhandlungen der geologischen Bundesanstalt, v. 56, p. 121-140.

Twitchett, R.J., Krystyn, L., Baud, A., Wheley, J.R., and Richoz, S., 2004, Rapid marine recovery after the end-Permian mass extinction event in the absence of marine anoxia: Geology, v. 32, p. 805-808.

Uhlig, V., 1881, Ueber die Fauna des rothen Kellowaykalkes der penninnischen Babierzówka bei Neumarkt in West-Galizien: Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt, v. 31, p. 381-422.

Urrutia, M.B., Iglesias, J.I.P., and Navarro, E., 1997, Feeding behaviour of *Cerastoderma edule* in a turbid environment: physiological adaptations and derived benefit: Hydrobiologia, v. 355, p. 173-180.

Van der Meer, J., Beukema, J.J., and Dekker, R., 2001, Long-term variability in secondary production of an intertidal bivalve population is primarily a matter of recruitment variability: Journal of Animal Ecology, v. 70, p. 159-169.

Velasco, L.A., and Navarro, J.M., 2002, Feeding physiology of infaunal (*Mulinia edulis*) and epifaunal (*Mytilus chilensis*) bivalves under a wide range of concentrations and qualities of seston: Marine Ecology Progress Series, v. 240, p.143-155.

Vermeij, G.J., 1977, The Mesozoic marine revolution: evidence from snails, predators, and grazers: Paleobiology, v. 3, p. 245-258.

Vermeij, G.J., 1987, Evolution and escalation: an ecological history of life: Princeton, Princeton University Press.

Vermeij, G.J., 1994, The evolutionary interaction among species: selection, escalation, and coevolution: Annual Reviews of Ecology and Systematics, v. 25, p. 219-236.

Vermeij, G.J., 1995, Economics, volcanoes, and Phanerozoic revolutions: Paleobiology, v. 21, p. 125-152.

Vogel, K., 1966, Eine funktionsmorphologische Studie an der Brachiopodengattung Pygope (Malm bis Unterkreide): Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 125, p. 423-442.

Vörös, A., 1973, Speculations on food supply and bathymetry in the Mediterranean Jurassic sea: Annales Universitatis Scientiarium Budapestinensis, Sectio Geologica, v. 16, p. 213-220.

Vörös, A., 1986, Brachiopod palaeoecology on a Tethyan Jurassic seamount (Pliensbachian, Bakony Mountains, Hungary): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 57, p. 241-271.

Vörös, A., 1991, Hierlatzkalk – a peculiar Austro-Hungarian Jurassic facies: Jubiläumsschrift 20 Jahre Geologische Zusammenarbeit Österreich – Ungarn, v. 1, p. 145-154.

Vörös, A., 1993, Jurassic microplate movements and brachiopod migrations in the western part of the Tethys: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 100, p. 125-145.

Vörös, A., 1995, Bathonian brachiopods of the Mecsek Mts (Hungary): Annales Univ. Sci. Budapest, Sect. Geol., v. 30, p. 181-208.

Vörös, A., 2005, The smooth brachiopods of the Mediterranean Jurassic: refugees or invaders?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 223, p. 222-242.

Vörös, A., Szabó, J., Dulai, A., Szente, I., Ebli, O., and Lobitzer, H., 2003, Early Jurassic fauna and facies of the Schafberg area (Salzkammergut, Austria): Fragmenta Palaeontogica Hungarica, v. 21, p. 51-82.

Wagenplast, P., 1972, Ökologische Untersuchung der Fauna aus Bank- und Schwammfazies des Weissen Jura der Schwäbischen Alb: Arbeiten aus dem Institut für Geologie und Paläontologie der Universität Stuttgart, N.F., v. 67, p. 1-99.

Waller, T.R., 1998, Origin of the molluscan class bivalvia and a phylogeny of major groups: *in* Johnston, P.A., and Haggart, J.W., eds., Bivalves: An eon of evolution – paleobiological studies honoring Norman D. Newell: University of Calgary Press, p. 1-45.

Walsh, J.A., 1996, No second chances? New perspectives on biotic interactions in post-Paleozoic brachiopod history: *in* Copper, P., and Jin, J., eds., Brachiopods: A.A. Balkema, Rotterdam, p. 281- 288.

Ward, P.D., Haggart, J.W., Carter, E.S., Wilbur, D., Tipper, H.W., Evans, T., 2001. Sudden productivity collapse associated with the Triassic-Jurassic boundary mass extinction: Science, v. 292, p. 1148-1151.

Warwick, R.M., 1988, Analysis of community attributes of the macrobenthos of Frierfjord/Langesundfjord at taxonomic levels higher than species: Marine Ecology-Progress Series, v. 46, p. 167-170.

Warwick, R.M., Clarke, K.R., and Gee, J.M., 1990, The effect of disturance by soldier crabs Mictyris platycheles H. Milne Erwards on meiobenthic community structure: Journal of experimental marine biology and ecology v. 135, p. 19-33.

Warwick, R.M., and Clarke, K.R., 1991, A comparison of some methods for analysing changes in benthic community structure: Journal of marine biological association of the United Kingdom v. 71, p. 225-244.

Wassmann, P., 1998, Retention versus export food chains: processes controlling sinking loss from marine pelagic systems: Hydrobiologia, v. 363, p. 29-57.

Webb, C.O., Ackerly, D.D., McPeek, M.A., and Donoghue, M.J., 2002, Phylogenies and community ecology: Annual Reviews in Ecology and Systematics, v. 33, p. 475-505.

Wendt, J., 1971, Genese und Fauna submariner sedimentärer Spaltenfüllungen im mediterranen Jura: Palaeontographica, v. 136A, p. 121-192.

Werner, W., Leinfelder, R.R., Fürsich, F.T., and Krautter, M., 1994, Comparative palaeoecology of marly coralline sponge-bearing reefal associations from the Kimmeridgian (Upper Jurassic) of Portugal and southwestern Germany: Courier Forschungsinstitut Senckenberg, v. 172, p. 381-397.

Whalen, M.T., Day, J., Eberli, G.P., and Homewood, P.W., 2002, Microbial carbonates as indicators of environmental change and biotic crises in carbonate systems: examples from the Late Devonian, Alberta basin, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 181, p. 127-151.

Whitney, F., Conway, K., Thomson, R., Barrie, V., Krautter, M., and Mungov, G., 2005, Oceanographic habitat of sponge reefs on the Western Canadian Continental Shelf: Continental Shelf Research, v. 25, p. 211-226.

Wierzbowski, A., Jaworska, M., and Krobicki, M., 1999, Jurassic (Upper Bajocian-lowest Oxfordian) ammonitico rosso facies in the Pieniny Klippen Belt, Carpathians, Poland: its fauna, age, microfacies and sedimentary environments: Studia Geologica Polonica, v. 115, p. 7-74.

Wierzbowski, A., Aubrecht, R., Krobicki, M., Matyja, B.A., and Schlögl, J., 2004, Stratigraphy and palaeogeographic position of the Jurassic Czertezik succession, Pieniny Klippen Belt (Western Carpathians) of Poland and eastern Slovakia: Annales Societatis Geologorum Poloniae, v. 74, p. 237-256.

Wignall, P.B., 1993, Distinguishing between oxygen and substrate control in fossil benthic assemblages: Journal of the Geological Society, London, v. 150, p. 193-196.

Williams, A., and Hurst, J.M., 1977, Brachiopod evolution: in Hallam, A. (ed.), Patterns of evolution as illustrated by the fossil record: Elsevier, Amsterdam, p. 79-121.

Wildish, D.J., and Kristmanson, D.D., 1984, Importance to mussels of the benthic boundary layer: Canadian Journal of Fisheries and Aquatic Sciences, v. 41, p. 1618-1625.

Wildish, D.J., Kristmanson, D.D., Hoar, R.L., DeCoste, A.M., McCormick, S.D., and White, A.W., 1987, Giant scallop feeding and growth responses to flow: Journal of Experimental Marine Biology and Ecology, v. 113, p. 207-220.

Wildish, D.J., and Miyares, M.P., 1990, Filtration rate of blue mussels as a function of flow velocity: preliminary experiments: Journal of Experimental Marine Biology and Ecology, v. 142, p. 213-219.

Willan, R.C., 1981, Soft-bottom assemblages of Paterson Inlet, Stewart Island: New Zealand Journal of Zoology, v. 8, p. 229-248.

Wilmsen, M., Blau, J., Meister, C., Mehdi, M., and Neuweiler, F., 2002, Early Jurassic (Sinemurian to Toarcian) ammonites from the central High Atlas (Morocco) between Er-Rachidia and Rich: Revue de Paleobiologie, v. 21, p. 149-175.

Woodin, S.A., 1976, Adult-larval interactions in dense infaunal assemblages: patterns of abundance:
Journal of Marine Research, v. 34, p. 25-41.

Woodin, S.A., 1983, Biotic interactions in Recent marine sedimentary environments: *in* Tevesz, M.J.S., and McCall, P.L., eds., Biotic interactions in recent and fossil benthic communities: Plenum Press, New York, p. 3-38.

Wright, S.H., 1982, A nutritional role for amino acid transport in filter-feeding marine invertebrates: American Zoologist, v. 22, p. 621-634.

Yamani, S.-A., 1975, Revision der Bivalvenfauna der Kelheimer Diceraskalke (Untertithon, Bayern): Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, v. 16, p. 5-10.

Zempolich, W.G., 1993, The drowning succession in Jurassic carbonates of the Venetian Alps, Italy: a record of supercontinental breakup, gradual eustatic rise, and eutrophication of shallow-water environments: AAPG Memoir, v. 57, p. 63-105.

Ziegler, V., and Michalík, J., 1980, Late Triassic serpulids (Annelids, Polychaeta, Sedentaria) in the West Carpathians: Geologický Zborník – Geologica Carpathica, v. 31, p. 627-640.

Zuschin, M., Stachowitsch, M., Pervesler, P., and Kollmann, H., 1999, Structural features and taphonomic pathways in the northern Gulf of Trieste, Adriatic Sea: Lethaia, v. 32, p. 299-317.