

BRACHIOPOD AND BIVALVE ECOLOGY IN THE LATE TRIASSIC (ALPS, AUSTRIA): ONSHORE-OFFSHORE REPLACEMENTS CAUSED BY VARIATIONS IN SEDIMENT AND NUTRIENT SUPPLY

ADAM TOMAŠOVÝCH*

Institut für Paläontologie, Würzburg Universität, Pleicherwall 1, 97070 Würzburg, Germany
e-mail: adam.tomasovych@mail.uni-wuerzburg.de

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 trends also occurred repeatedly on a short time scale and mainly were driven by variations in sediment and nutrient supply. In the Kössen Formation (Upper Triassic), brachiopods retreated to offshore habitats during nutrient-rich, siliciclastic regimes and expand to onshore habitats during nutrient-poor, carbonate regimes. Epifaunal bivalves occupied onshore and offshore habitats during both siliciclastic and carbonate regimes. Infaunal suspension-feeding bivalves expanded to offshore habitats during nutrient-rich, siliciclastic regimes and retreated from offshore habitats during nutrient-poor, carbonate regimes. Thus, the onshore to offshore retreat of brachiopods and the offshore expansion of infaunal bivalves repeatedly coincided with the switch from a nutrient-poor, carbonate regime to a nutrient-rich, siliciclastic regime. Because 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.

Differences in guild structure between siliciclastic and carbonate regimes and onshore to 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 low metabolic demands and are 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 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 to 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 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 evaluated rigorously, two environmental trends and one taphonomic trend can be coupled with the 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), they are now largely restricted to some specific habitats in modern seas, such as shaded fjords, caves, or polar regions (Jackson et al., 1971; James et al., 1992; Rhodes and Thompson, 1993). Although dense populations of modern brachiopods are known locally from tropical-shelf habitats (Kowalewski et al., 2002), the retreat from onshore habitats 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 rarely are dominated by brachiopods in terms of abundance or diversity, or by other immobile epifaunal suspension-feeders (e.g., free-living bivalves) in terms of community-level abundance (LaBarbera, 1981a; Jablonski and Bottjer, 1983). Brachiopods mainly are 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 understanding community-level history of brachiopods also depends 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 a 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).

Many brachiopod clades that 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 global diversity trajectories might indicate that the decline of brachiopods has been caused almost exclusively by the end-Permian mass extinction (Gould and Calloway, 1980; Sepkoski, 1996), this is not supported by their community-level abundances. Brachiopods, as a group (mainly represented by rhynchonellids and terebratulids), again became 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). Because 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, because 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 the Mesozoic and Cenozoic might not be explained by the end-Permian mass extinction alone. Note that brachiopod clades that dominated in shallow habitats and coral

* Current address: Geological Institute, Slovak Academy of Sciences, Dúbravská cesta 9, 840 05 Bratislava, Slovakia.

¹ www.sepm.org/archive/index.html

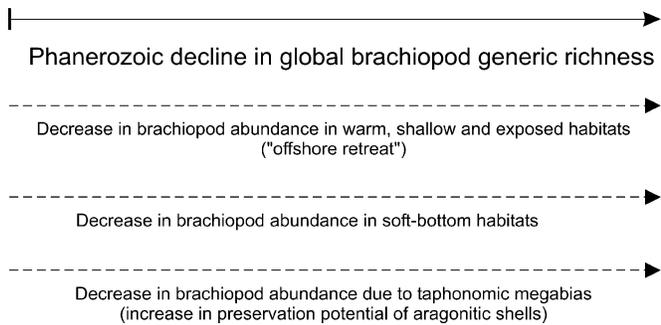


FIGURE 1—Two simplified trends in environmental distribution of brachiopods and one taphonomic trend, which can be associated with their Phanerozoic decrease in generic richness. It remains to be evaluated quantitatively whether these trends are real and whether they are gradual or stepwise.

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 as to which environmental circumstance allows 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 brachiopod distribution. Present-day rhynchonelliformean brachiopods mainly are 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 the 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, it is supposed that the high metabolic demands of bivalves are not fulfilled, whereas the low metabolic demands of brachiopods are met (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 a 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 associated with a shelf-break where upwelling waters rich in dissolved nutrients are found (Kowalewski et al., 2002; Rodland et al., 2004). Such nutrient-rich habitats can be characterized by low oxygen levels, relatively cold temperatures, or other factors that may be limiting 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 that increase the cost of a high-energy metabolism. However, quantitative analyses of compositional variations of bivalve and brachiopod communities along an environmental gradient that could test this actualistic hypothesis are rare (i.e., do brachiopods increase in abundance relative to bivalves along a decreasing nutrient-supply gradient?).

An ideal way to investigate the coexistence of brachiopods and bivalves in the fossil record 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 were not yet restricted to refugia habitats, and bivalves were dominant 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 these groups were not dominant brachiopods in Late Paleozoic communities, their abundance in Triassic habitats is difficult to explain as a relatively short-term resurgence of otherwise refugia-restricted taxa due to 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 brachiopod community-level abundance can be explained by substrate variations alone, and if their distribution correlates with nutrient-supply and turbidity gradients.

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 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 probably is 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 meter-scale, siliciclastic-carbonate sequences 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 to wavy mm-scale lamination in their lower part, and abundant limestone beds with hummocky cross-stratification (HCS) in their upper part. The carbonate intervals consist of thick limestone beds with corals, sponges, and megalodont bivalve shell beds with locally oolitic beds in their lower parts, and brachiopod-bivalve rudstones, floatstones, or pavements in their upper parts. The Eiberg Member consists of sequences with marls, marlstones, and mudstones, locally with bioturbated wackestones and floatstones with no signs of storm reworking. Based on thickening-upward limestone beds, an asymmetric trend in the calcareous/siliciclastic ratio, and corresponding variations in palynofacies composition (Hüssner et al., 2000; Holstein, 2004), these beds also can be 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 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 shallower conditions/higher storm activity compared to the marlstones and planar/wavy laminated mudstones in the lower part. However, deposits in the carbonate intervals commonly show a high proportion of micritic matrix, and indicate depths both above and below NSWB (i.e., they are not consis-

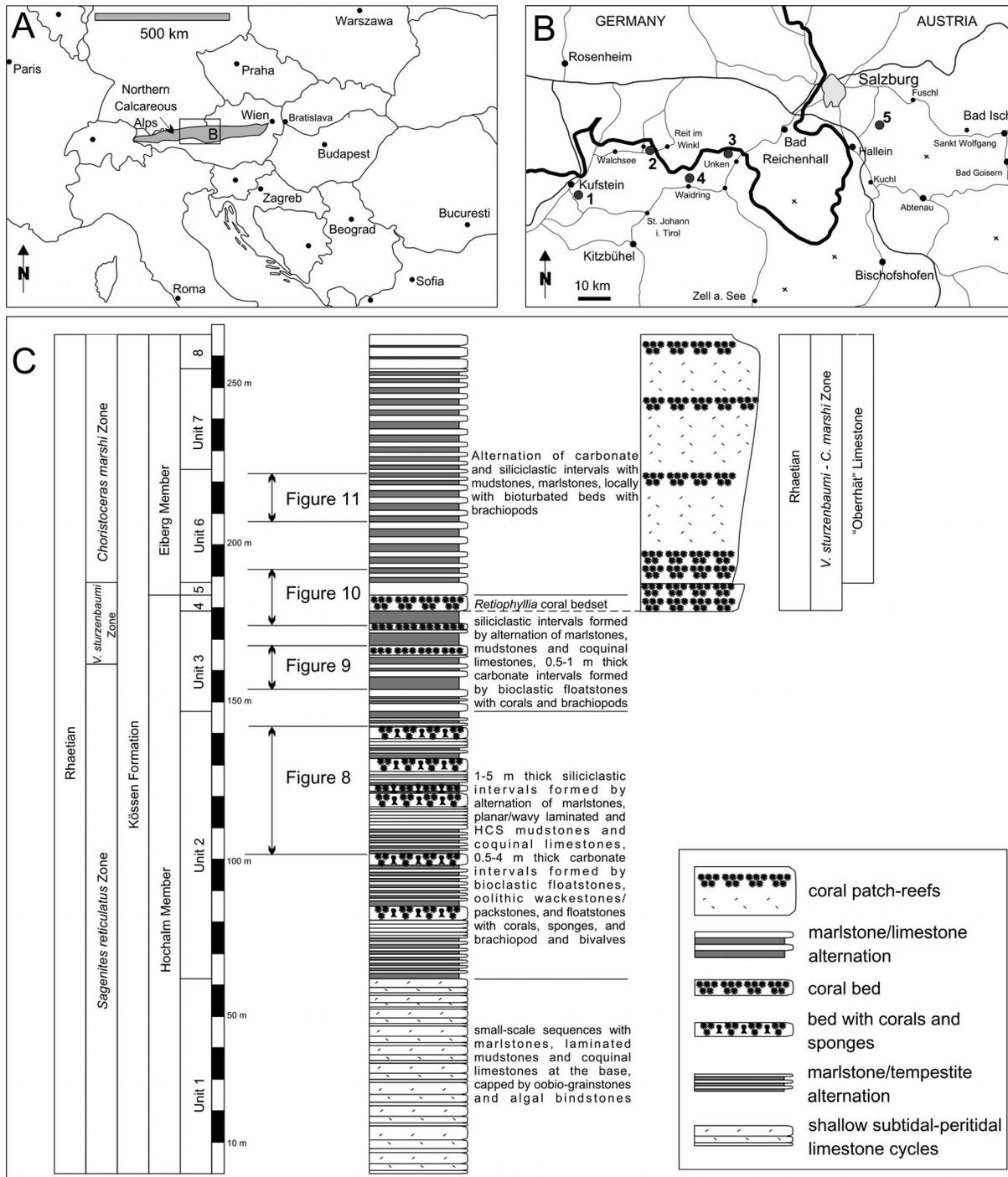


FIGURE 2—Locality map and stratigraphic section. (A) Geographic location of the Northern Calcareous Alps. (B) Geographic location of sections in the Northern Calcareous Alps. (C) Schematic section of the Kössen Formation, with its stratigraphic subdivision based on Golebiowski (1990).

tently shallower, as would be predicted by the shallowing-upward trend). In contrast to the upper part of the siliciclastic intervals, which indicate depths above normal storm wave base (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 and/or a decrease in carbonate production. A thick marlstone in the middle 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 also is 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 rates of siliciclastic and carbonate supply, possibly driven by climatic changes alone (Burgess,

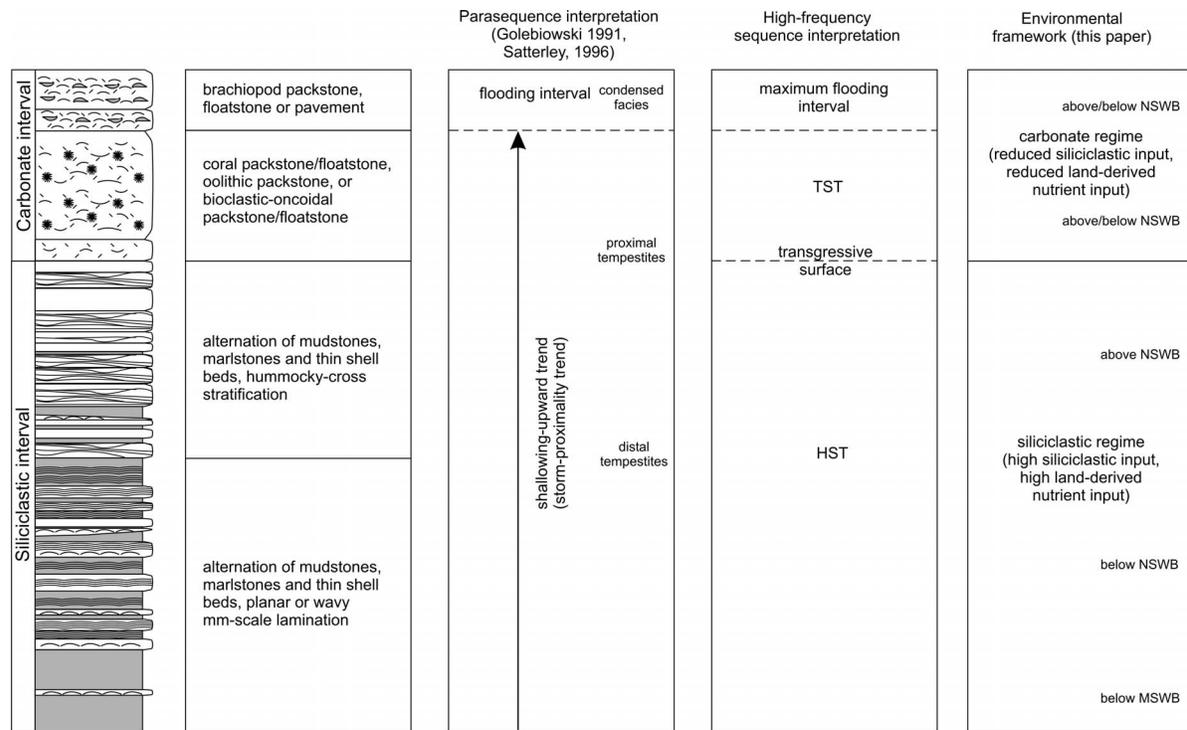


FIGURE 3—Schematic section through small-scale, siliciclastic-carbonate sequence with possible interpretations, and environmental framework used in this paper.

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.

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

METHODS

Data Analyses

Sixty-five samples derived from five sections in the Northern Calcareous Alps (Fig. 2) were analyzed. Although benthic components, such as corals, sponges, gastropods, and crinoids, can be present locally, only brachiopods and bivalves were included in the analyses. All determinable brachiopods and bivalves larger than 2–3 mm were sampled mechanically from lithified or poorly lithified rocks. In addition, nine samples were used from the dataset of Golebiowski (1989), which is based on similar sampling protocol. The samples encompass the Kössen Formation with the exception of the lowermost unit. All but five samples contain more than 25 specimens (see Supplementary Data 1¹). The five samples that have >10 but <25 specimens were included in the analysis because they contain brachiopod taxa, which are rare or absent in other samples. Taxonomic identifications were based on Pearson (1977), Michalík (1977), Golebiowski (1989), and Siblík (1998). Absolute abundances were converted into number of individuals with the minimum number of individ-

uals (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 is preferable because some bivalves show preferential preservation 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 paleo-community 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. Based on the Bray-Curtis coefficient, ANOSIM tests whether within-habitat average-rank dissimilarity is significantly lower than between-habitat average-rank dissimilarity (Clarke and Green, 1988). If the null hypothesis (i.e., no differences in composition between habitats) is rejected, the differences in composition among habitats cannot be explained by chance. The statistical value R potentially ranges from -1 to 1 . If $R = 1$, the habitats are completely different in composition; if $R = 0$, the within-habitat average rank dissimilarity is not less than the between-habitat average rank dissimilarity. If $R = -1$, the rank dissimilarities between habitats are invariably smaller than those within habitats. Monte Carlo randomization was used for estimating the significance level.

ANOSIM is complemented by non-metric multidimensional scaling (NMDS), which ordines samples according to their dissimilarity in species 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 leads to creation of 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). Although NMDS does not quantify the length of ecologic gradients 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 interrelationship of assemblages (Shi, 1993). With increasing species

turnover along environmental gradients and increasing complexity of ecologic gradients that control species abundances, NMDS is a preferable ordination method for visualizing differences in community composition among habitats (Kenkel and Orlóci, 1986; McCune et al., 2002). In this paper, NMDS was computed with Kruskal's algorithm (1964), which was repeated twenty times with different random positions of samples in starting configurations.

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). Results of this study do not vary substantially when untransformed relative abundances are used. The role of transformations in multivariate community analyses mainly is related to differential weighting of abundant and rare species in computing similarities (Clarke and Warwick, 2001). The square-root transformation has the effect of down-weighting the importance of highly dominant species so that similarities also depend on relative abundance of less-common species. It can be considered as a moderate transformation because fourth-root, logarithmic, or presence/absence transformations would lead to more severe down-weighting of abundant species.

ANOSIM tested the differences in community composition among the following three depth habitats, which were determined using 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 to wavy, mm-scale laminated beds in the siliciclastic intervals and by floatstones and wackestones reflecting alternations 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 (see Supplementary Data 2¹). Note that this protocol reflects both structures of sampled beds and their sedimentologic context within sequences. For example, if several mm-thick packstones formed by winnowed shell pavements are embedded within homogeneous marlstones, the sample is assigned to the habitat below MSWB. If such a pavement alternates with planar-to-wavy laminated mudstones and other pavements, it is assigned to the habitat between NSWB and MSWB. Testing was performed separately for the carbonate and siliciclastic intervals. If carbonate and siliciclastic intervals were not easily 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 (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 rarely were considered in paleoecologic analyses (but see McRoberts and Newton, 1995; McRoberts et al., 1995). However, actualistic evidence indicates that different gill types correspond to distinct feeding strategies with respect to the quality and quantity of nutrient supply (i.e., they differ in clearance and rejection rates under varying particle concentrations). Therefore, the bivalve guilds were subdivided according to their gill type using 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 were subdivided further 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 a filibranch gill, and deep burrowers by an eulamellibranch gill; see Supplementary Data 3¹). Brachiopods are dif-

ferentiated into pedunculate and free-lying guilds (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 a strongly incurved ventral beak with a 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 are dominated by brachiopods. Six bivalve sample groups are dominated by infaunal bivalves (*Isocyprina* and *Myophoriopsis*), semi-infaunal bivalves (*Bakevella* 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.

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 continuously pass into each other, indicating that the compositional gradient has been dissected arbitrarily 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 that also occur in other bivalve and brachiopod sample groups (e.g., *Atrreta*, *Rhaetavicularia*, and *Gervillaria*). *Rhaetina gregaria* also occurs in the brachiopod-dominated *R. pyriformis* sample group. Other brachiopod species occur in brachiopod-dominated sample groups almost exclusively.

Q-mode NMDS based on guild composition shows mostly good separation among the sample groups dominated by different guilds (Fig. 7B), indicating that differences in guild composition are consistent. 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 also is some overlap between the sample groups dominated by pedunculate brachiopods and epifaunal bivalves (Fig. 7B). In turn, sample groups dominated by epifaunal bivalves show partial overlap with the sample groups dominated by infaunal bivalves. Sample groups with infaunal and semi-infaunal bivalves also are segregated. R-mode NMDS based on species shows that although there is some overlap among bivalve and brachiopod species, brachiopods tend to coexist more commonly with other brachiopods than with bivalves (Fig. 7C). R-mode NMDS of guilds shows that both pedunculate and free-lying brachiopods coexist 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.

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 separately for Unit 2, Unit 3, and units 4–8 (below). 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). Carbonate intervals are dominated by brachiopods and some epifaunal bivalves (*R.*

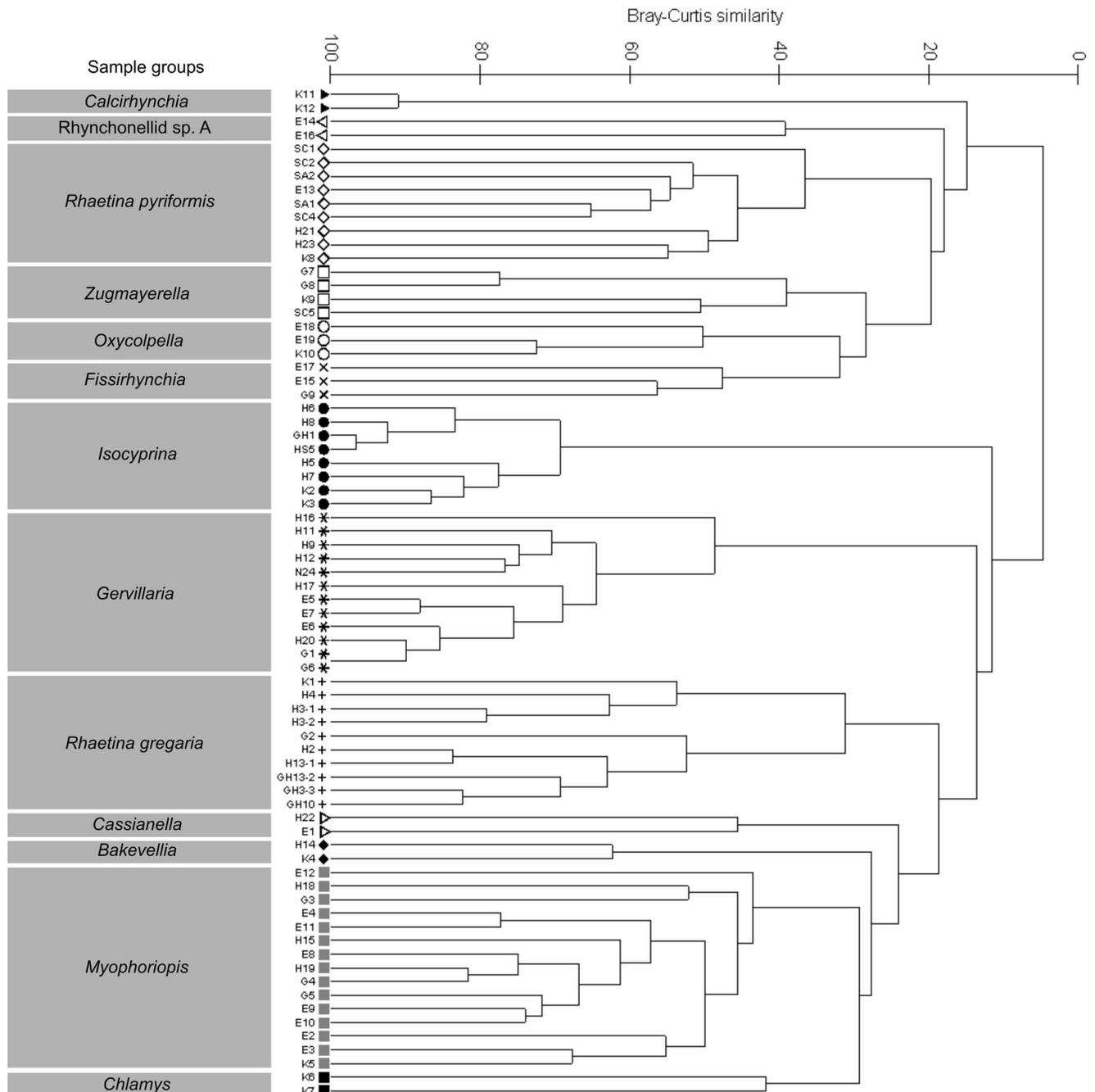


FIGURE 4—Cluster analysis of the samples, leading to discrimination of 13 sample groups.

gregaria sample group), in contrast to the siliciclastic intervals, which are dominated by infaunal (*Isocyprina* sample group) and semi-infaunal bivalves (*Gervillaria* sample group, Fig. 8). Epifaunal bivalves also occur 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 only in the carbonate intervals, thus 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.

COMMUNITY VARIATION ALONG AN ONSHORE-OFFSHORE GRADIENT

Compositional variation of the sample groups and differences in species and guild composition between the depth habitats are analyzed with NMDS. In addition, ANOSIM is 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.

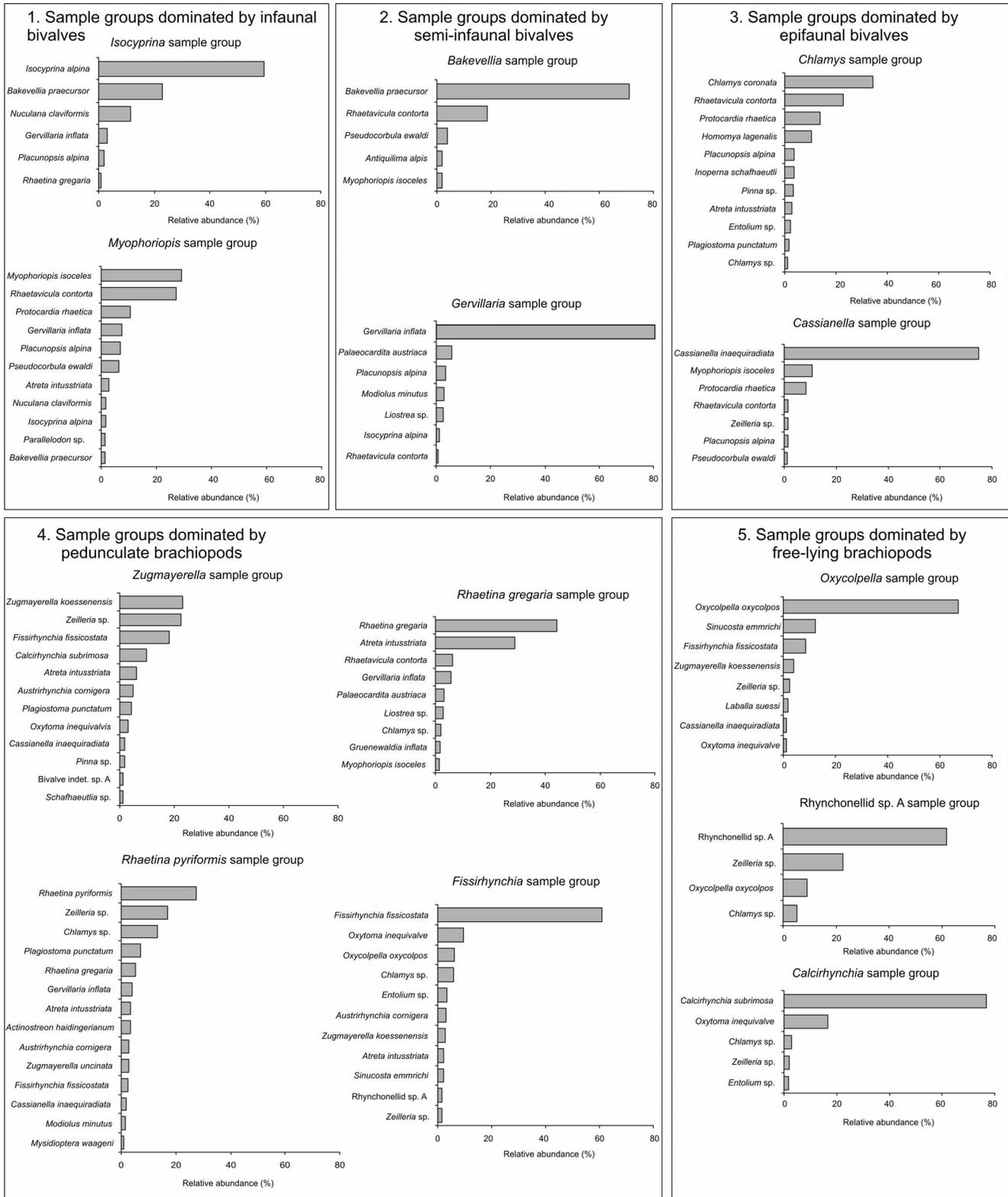


FIGURE 5—Relative abundances of species in the 13 sample groups identified in Figure 4. Species < 1% are excluded.

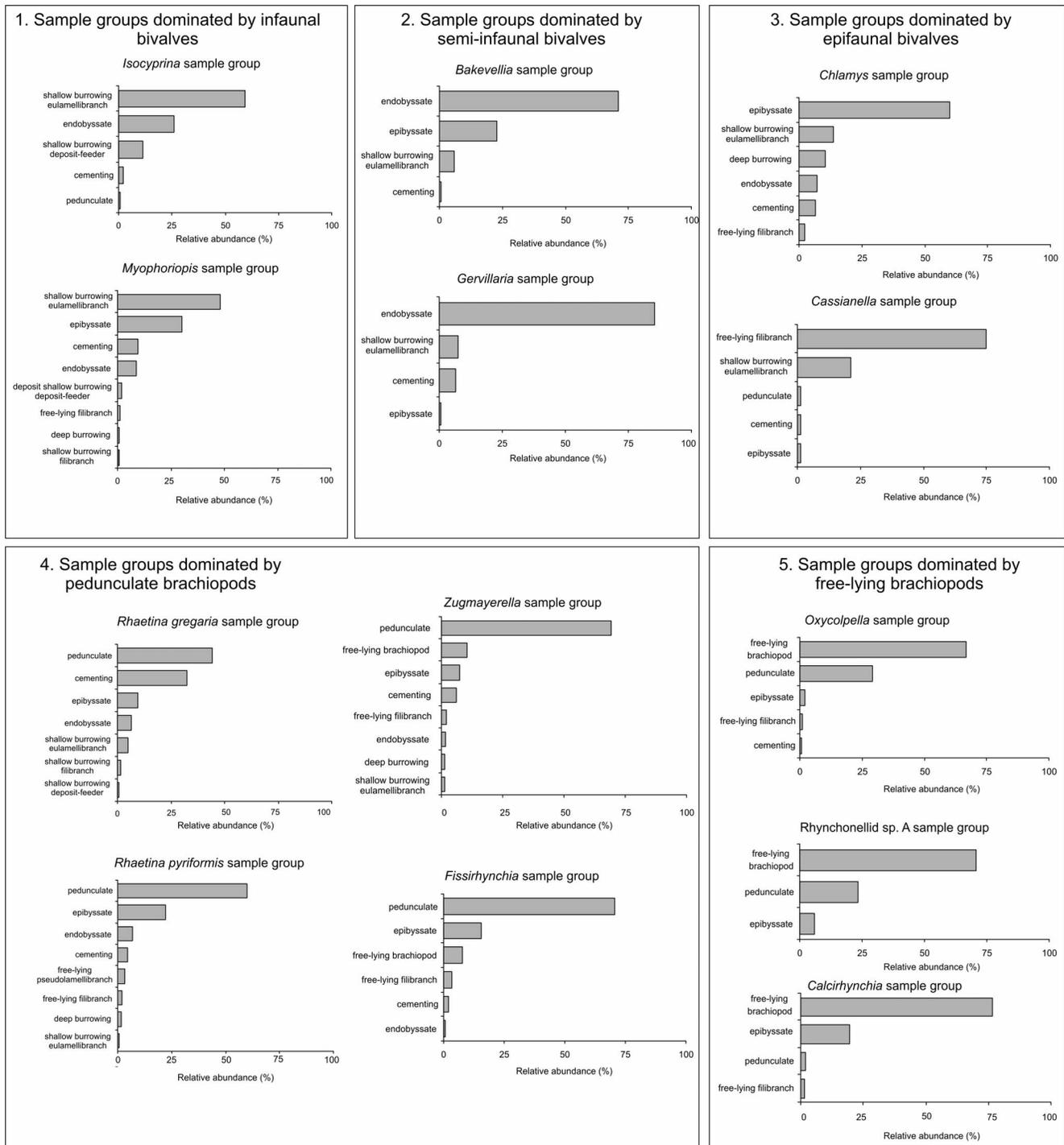


FIGURE 6—Relative abundances of guilds in the 13 sample groups identified in Figure 4. All guilds are shown.

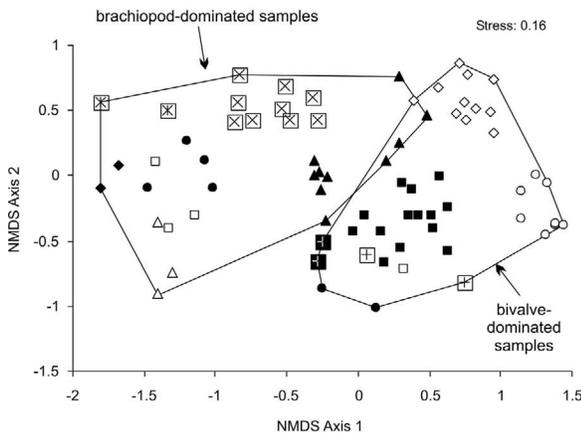
Onshore-Offshore Gradient of Unit 2

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. Between-habitat differences also are apparent in NMDS (Fig. 12A). Similarly, compositional segregation for three depth habitats follows from the guild composition (Table 2, Fig. 12B). 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 endobysate *Gervillaria* (Fig. 13). Habitats below NSWB, associated with deposits exhibiting pla-

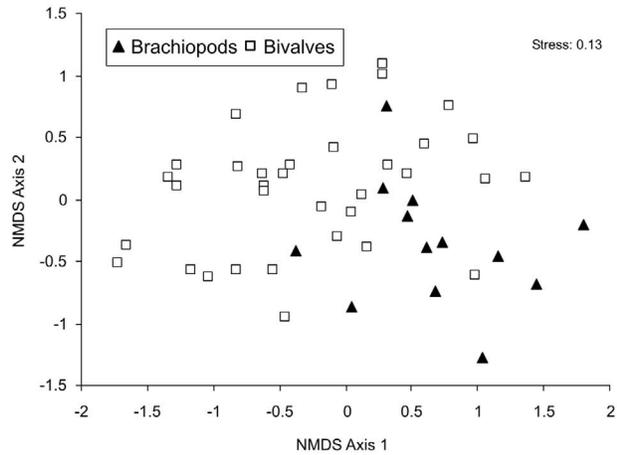
nar or wavy mm-scale stratification in the lower parts of the siliciclastic intervals, are dominated by shallow-infaunal eulamellibranch bivalves (*Isocyprina* sample group). Although the two samples that are dominated by pedunculate brachiopods (*R. gregaria* sample group) occur in single-event packstones, like 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).

Carbonate Intervals: Because the number of samples from the carbonate intervals is very low, the p -values are inconclusive (Table 2, Fig. 12C,

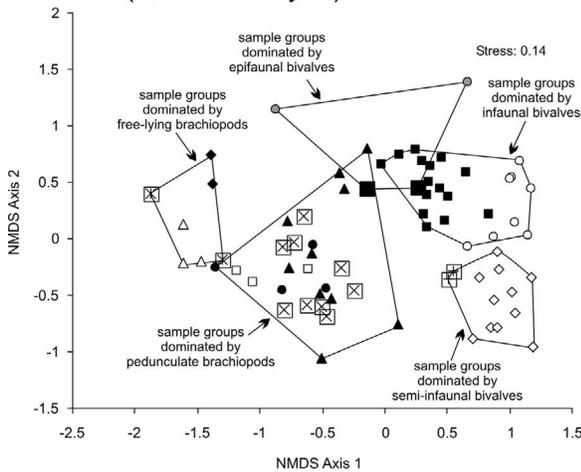
A. Species (Q-mode analysis)



C. Species (R-mode analysis)



B. Guilds (Q-mode analysis)



D. Guilds (R-mode analysis)

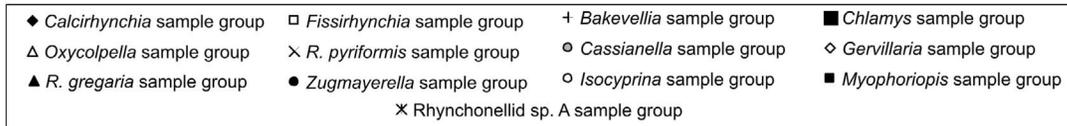
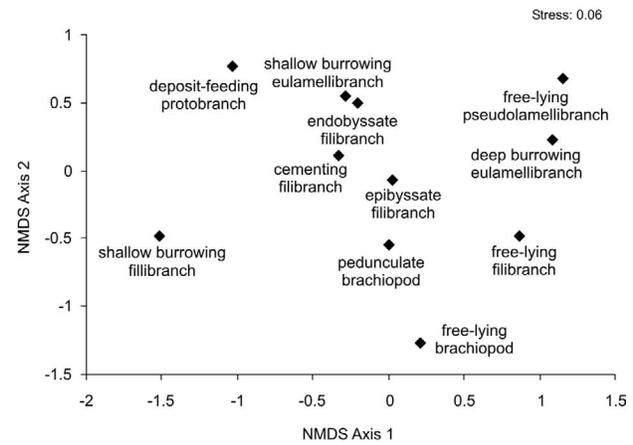


FIGURE 7—Non-metric multidimensional scaling (NMDS) analyses. (A) Q-mode analysis of samples based on species composition. (B) Q-mode analysis of samples based on guild composition. (C) R-mode analysis of species. (D) R-mode analysis of guilds.

TABLE 1—Results of ANOSIM tests for 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).

	R Statistic	P-value	Permutations	Number of permuted R \geq 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

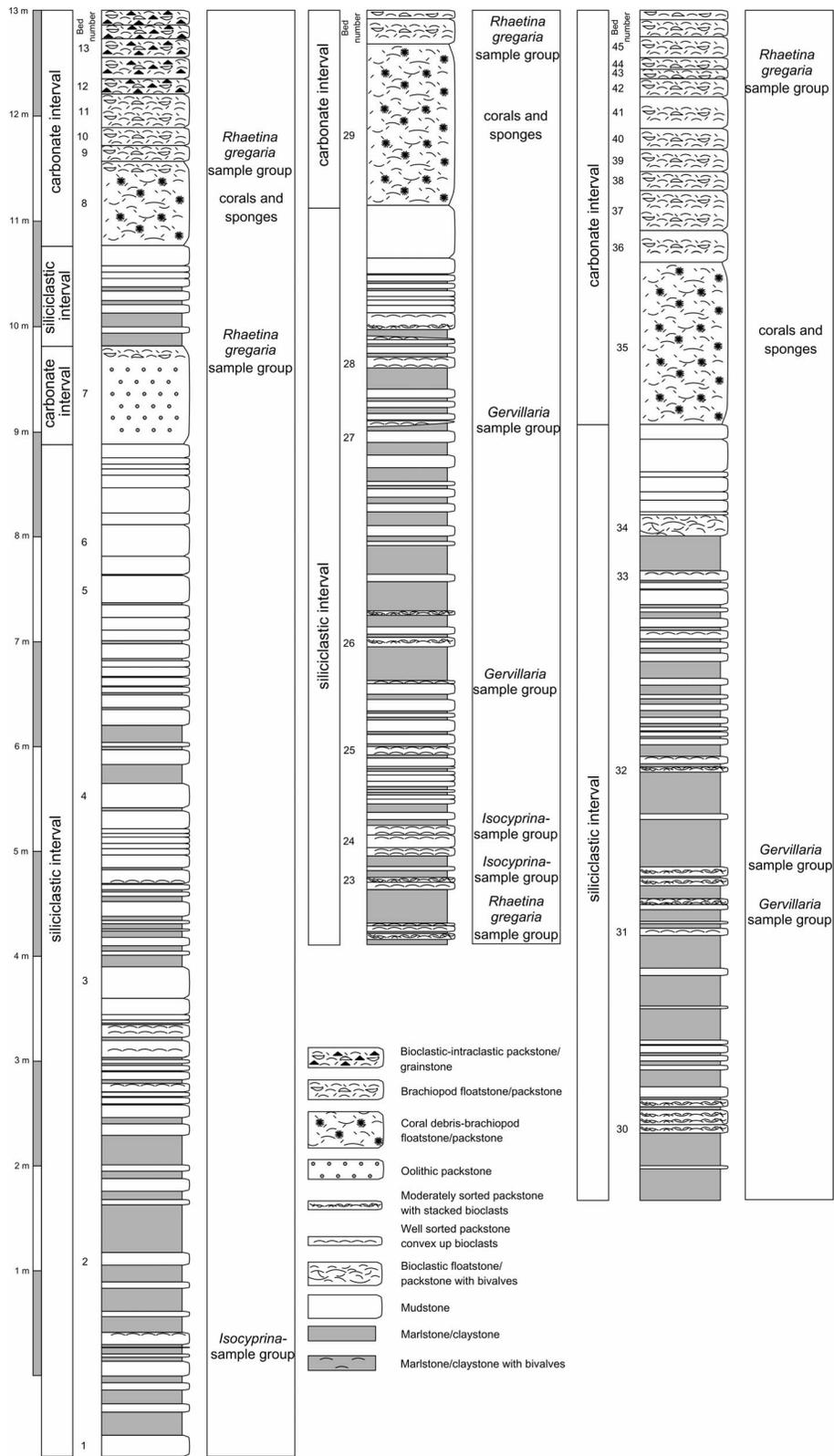


FIGURE 8—Stratigraphic distribution of sample groups in Unit 2 of the Hochalm Member. The three segments represent successive parts of the section at Hochalm and record four siliciclastic-carbonate sequences.

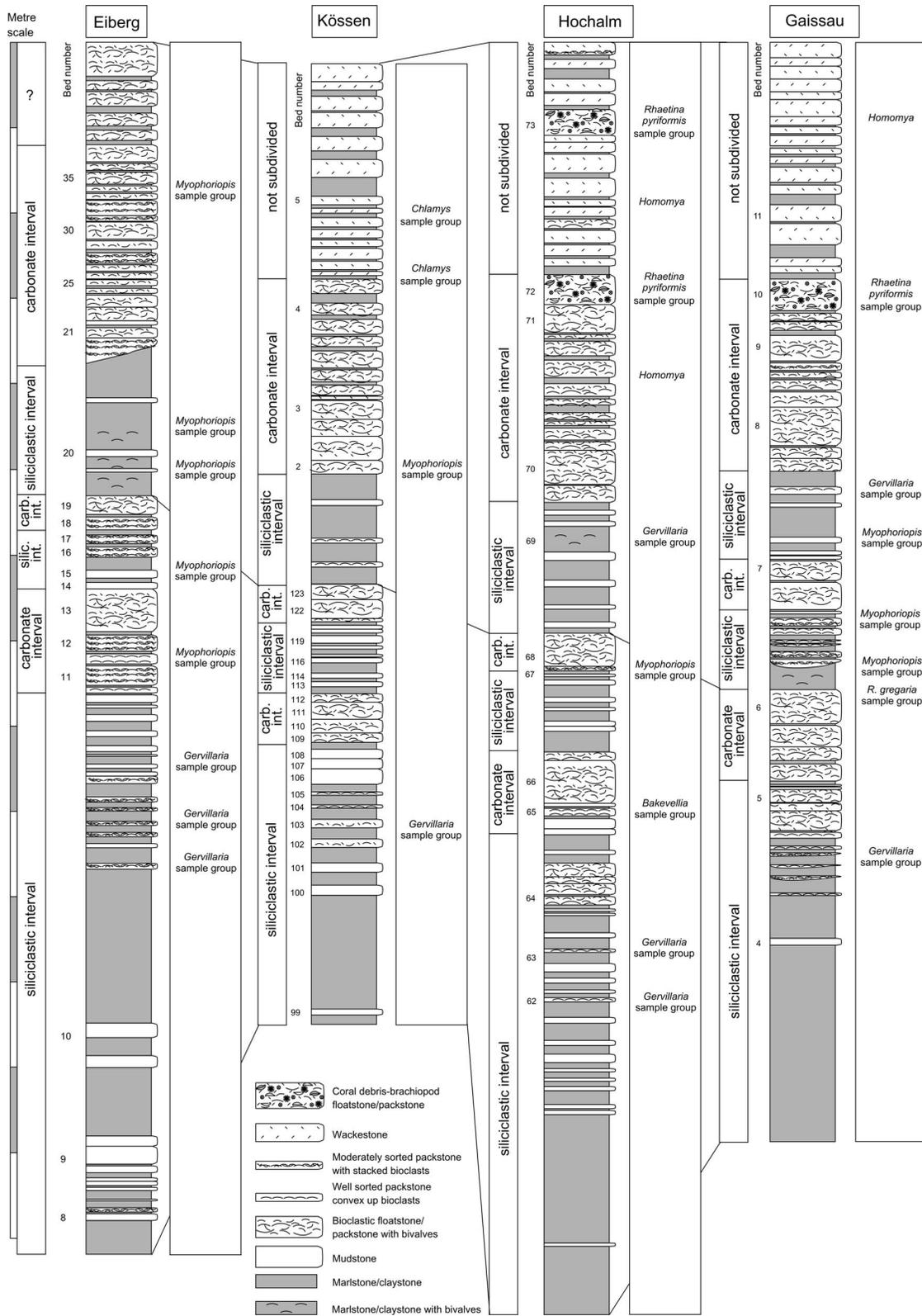


FIGURE 9—Stratigraphic distribution of sample groups in Unit 3 of the Hochalm Member. The four sections represent stratigraphically equivalent segments of the lower parts of Unit 3 (see correlation lines). The occurrence of the bivalve *Homomya*, typical of the *Chlamys* sample group, is shown for several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

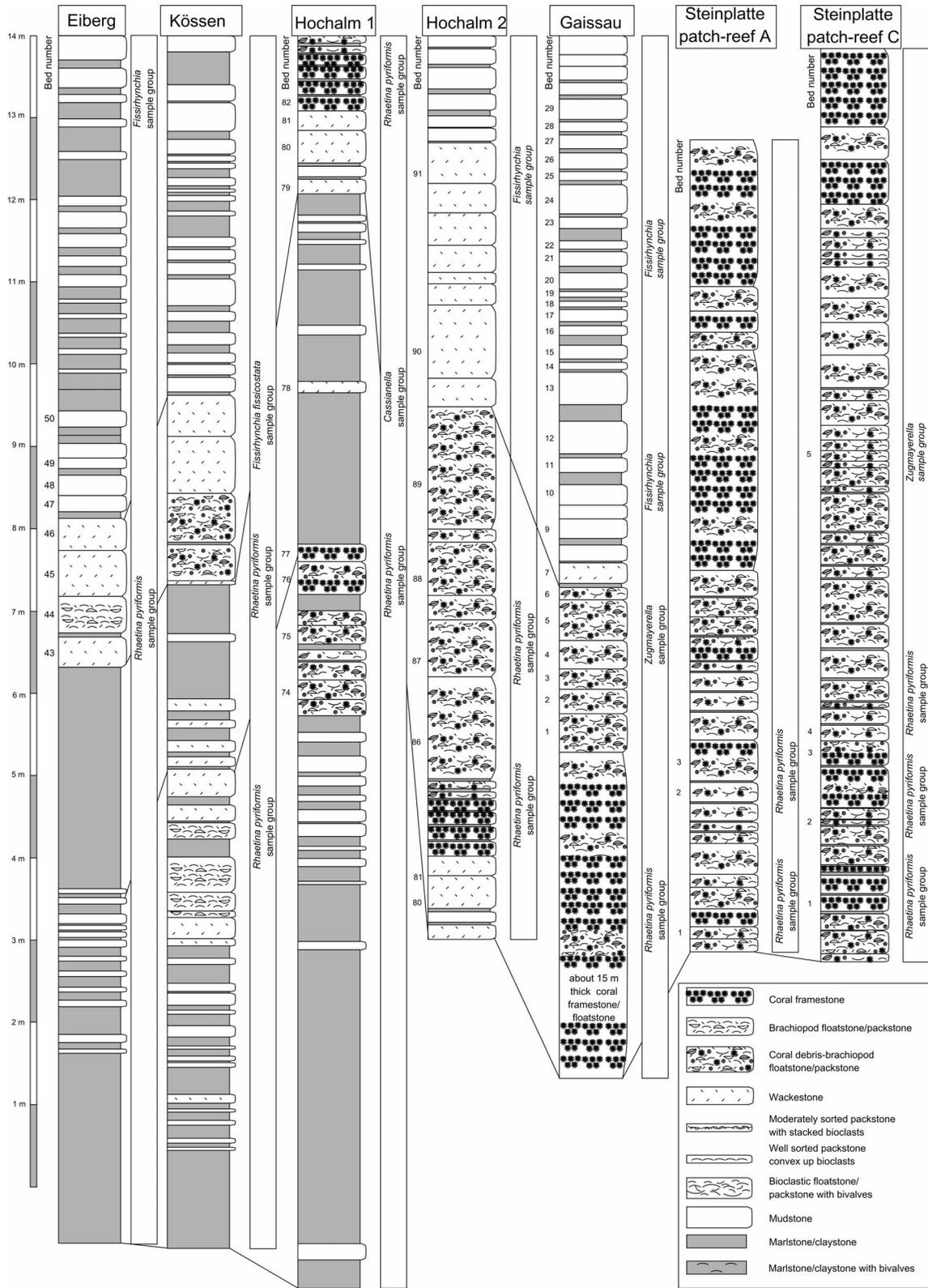


FIGURE 10—Stratigraphic distribution of sample groups in the upper parts of the Hochalm Member and the lowermost part of the Eiberg Member. The six sections show a lateral transition from basinal environments (Eiberg, Kössen, Hochalm, and Gaissau) into patch-reefs at Steinplatte (see correlation lines).

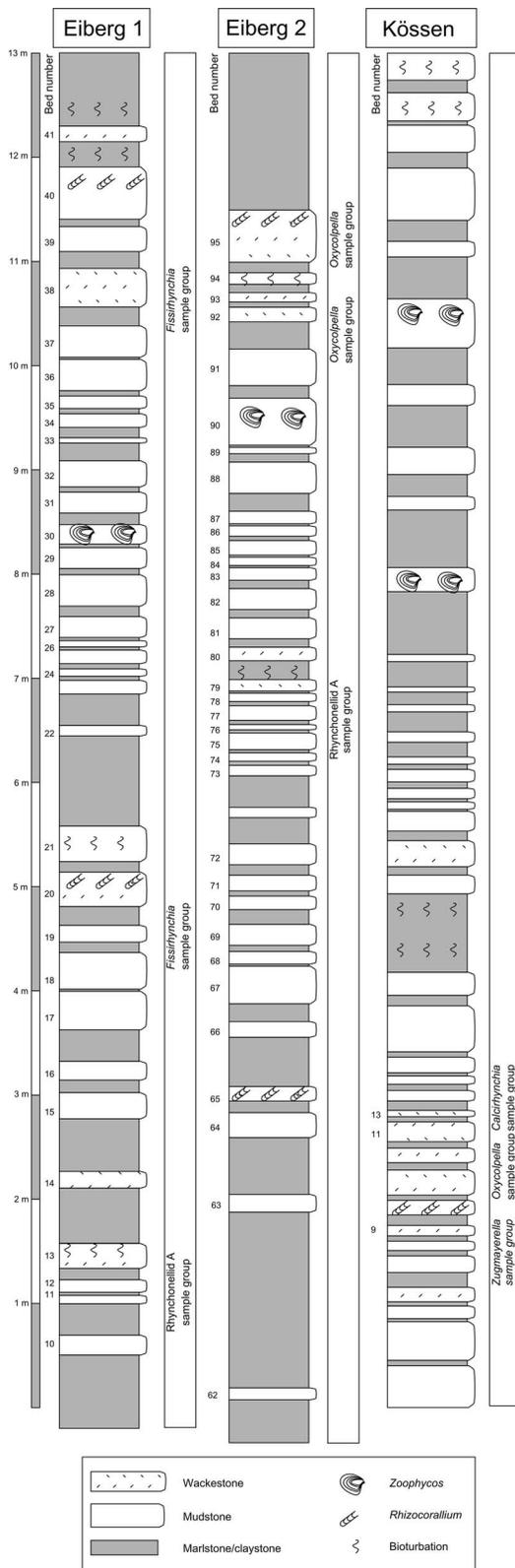


FIGURE 11—Stratigraphic distribution of sample groups in three sections of the middle part of the Eiberg Member (Unit 6). Brachiopod sample groups occur in the carbonate-rich intervals characterized by dominance of limestone beds.

D). In the onshore-offshore gradient, habitats above NSWB are represented by bioclastic packstones and coral floatstones with internal storm stratification, and habitats below NSWB are represented 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 FWFB. 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 the onshore direction may have been dominated by the bivalve *Placunopsis alpina* or by megalodonts because the carbonate intervals are replaced in a landward direction by deposits that represent restricted carbonate lagoons and tidal flats (Golebiowski, 1991).

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). Pairwise differences in species and guild composition between the particular depths are always of high or borderline significance (Table 3). Habitats above NSWB are dominated by the endobyssate *Gervillaria*, which occurs in thin shell beds and as pavements in beds with hummocky cross-stratification (Fig. 15). The shallow-burrowing *Myophoriopsis* is typical of the habitats below NSWB (Fig. 15). Epibyssate and cementing bivalves also are common in the habitats below NSWB. The *Cassianella* and *Chlamys* sample groups, which are dominated by epifaunal bivalves, typically occur in marlstones and mudstones below MSWB. The soft-bottom, siliciclastic-rich habitats below MSWB thus are dominated by epibyssate and free-lying filibranchs (Fig. 15).

Carbonate Intervals: NMDS shows only partial compositional overlap between habitats below and above NSWB (Fig. 14C, D). ANOSIM shows that 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). Habitats above NSWB are dominated by shallow-burrowing eulamellibranchs and epibyssate, endobyssate, and cementing guilds. Habitats below NSWB are dominated either by shallow-burrowing eulamellibranchs, or by pedunculate brachiopods. However, the *Rhaetina pyriformis* sample group, which is dominated by pedunculates and epifaunal bivalves, is limited to the habitats below NSWB. In contrast to the beds with *Myophoriopsis* and *Bakevellia*, beds with *R. pyriformis* lack complex internal stratification, which would point to episodic storm events. 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 *Myophoriopsis* and *Bakevellia* mostly are 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 coexistence of bivalve and brachiopod communities along one bathymetric transect is indicated by the presence of the *Myophoriopsis* 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 a reduced sediment supply (Fig. 15).

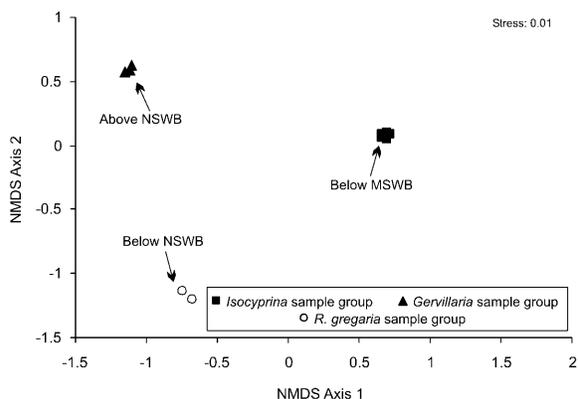
Onshore-Offshore Gradient of Units 4–8

Siliciclastic Intervals: No quantitative samples are available from the siliciclastic-rich intervals of the Eiberg Member, which mostly are devoid of shelly benthic fauna. Golebiowski (1989) noted rare finds of epifaunal

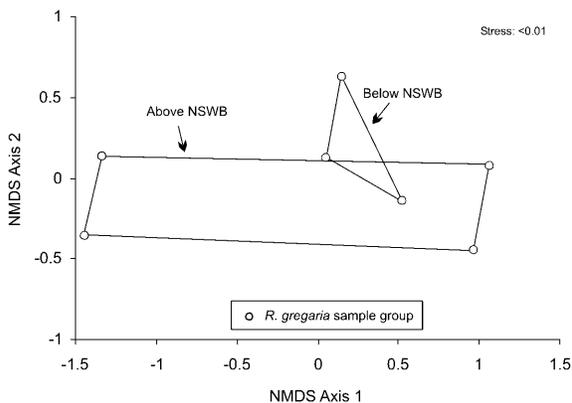
TABLE 2—Results of ANOSIM tests for differences in species and guild composition in different bathymetric settings of Unit 2. The tests are performed separately for the carbonate and siliciclastic intervals. The Bonferroni correction lowers the alpha value in pairwise tests to 0.017 (0.05/3). The p-values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

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

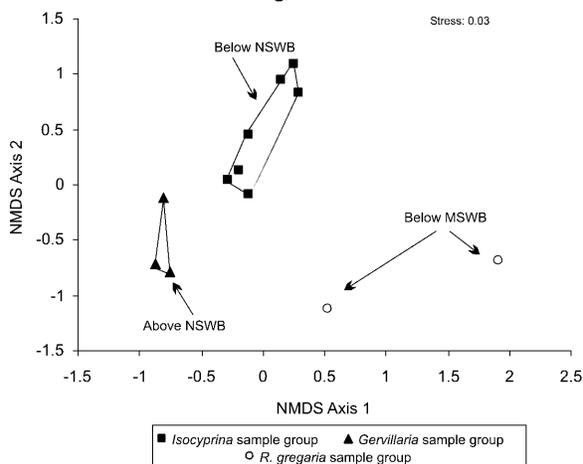
A. Siliciclastic intervals - species



C. Carbonate intervals - species



B. Siliciclastic intervals - guilds



D. Carbonate intervals - guilds

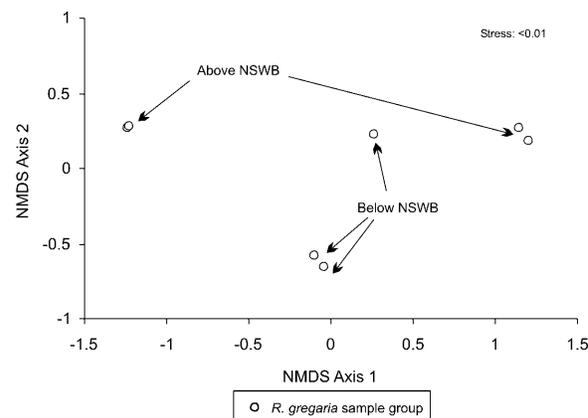


FIGURE 12—Ordination of samples of Unit 2 showing between-habitat differences in species and guild composition. (A) Siliciclastic intervals—Q-mode NMDS based on species composition. (B) Siliciclastic intervals—Q-mode NMDS based on guild composition. (C) Carbonate intervals—Q-mode NMDS based on species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

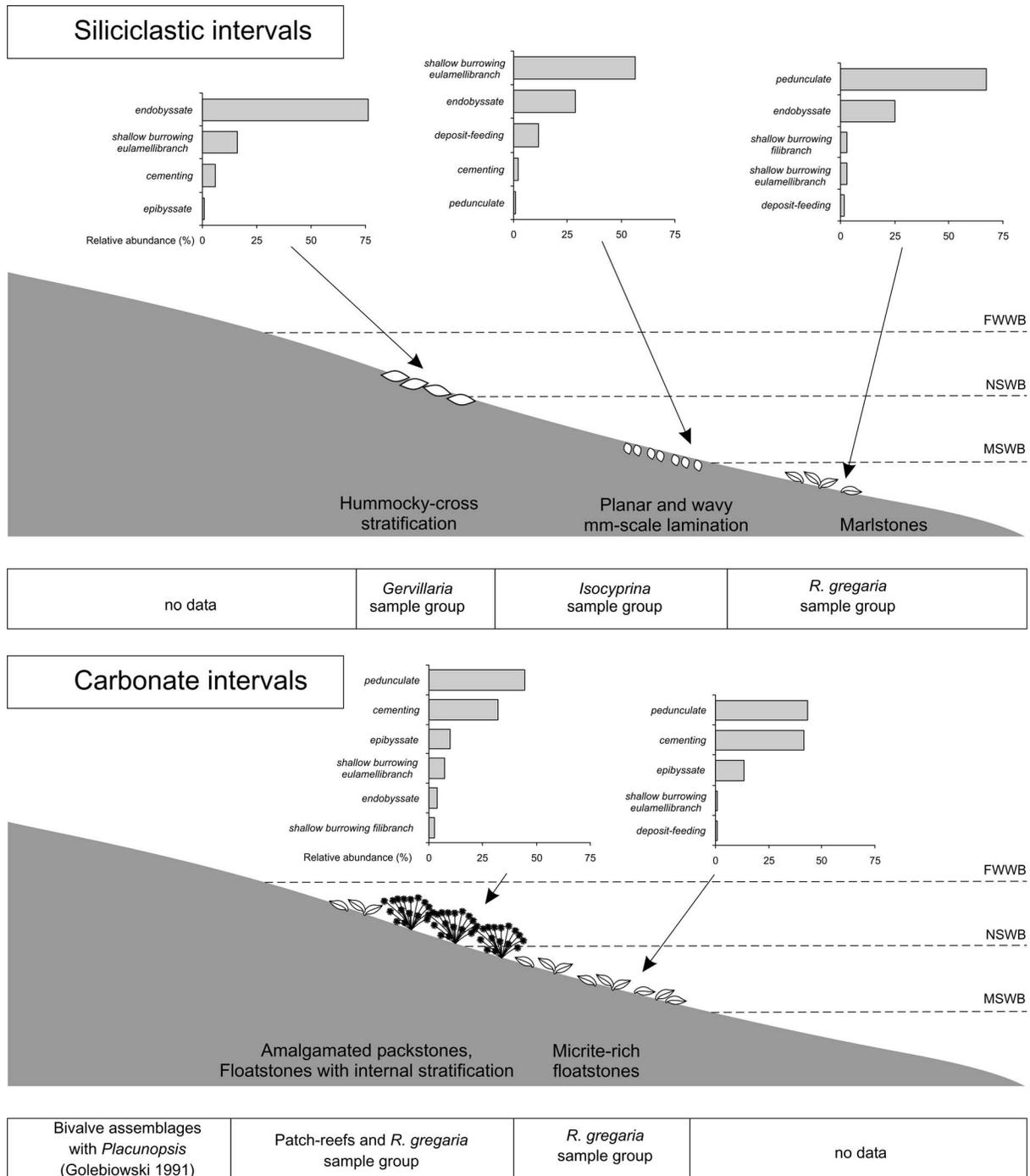


FIGURE 13—Distribution of sample groups along an onshore-offshore gradient in Unit 2. (A) Siliciclastic intervals; note that bivalves dominate in shallow habitats and brachiopods in deep habitats. (B) Carbonate intervals; note that brachiopods dominate in shallow habitats above NSWB.

bivalves (*Oxytoma*) and brachiopods (rhynchonellids and *Oxycolpella*), which are equivalent to the species known from the carbonate intervals of the Eiberg Member. Most 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 most probably is a 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 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 epibysate, endobysate, and cementing bivalves. Soft-bottom habitats below MSWB were dominated either by pedunculate brachiopods (*Fissirhynchia*) or free-living brachiopods (Fig. 17; *Oxycolpella* and rhynchonellids). Deposits

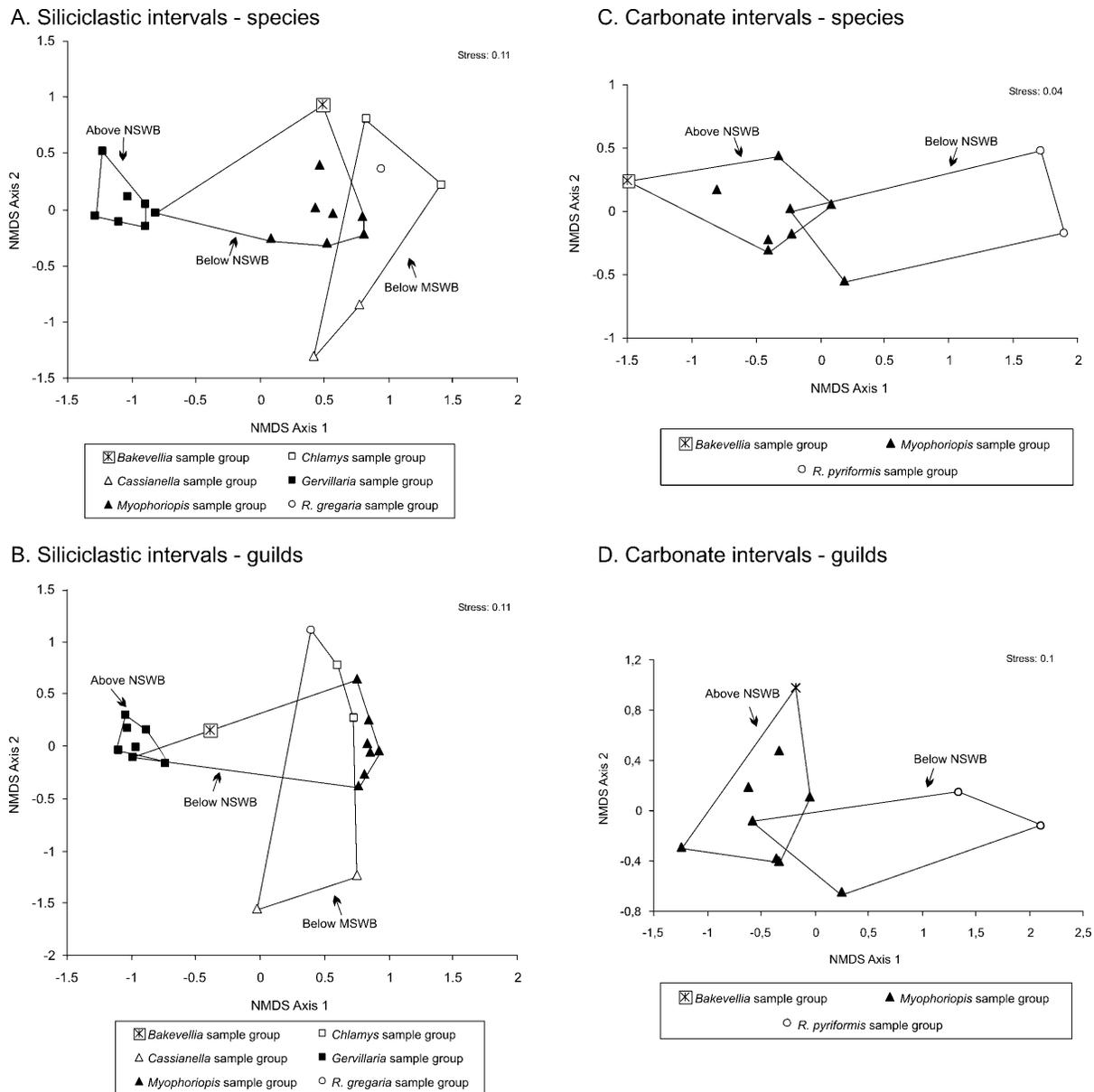


FIGURE 14—Ordination of samples of Unit 3 showing between-habitat differences in species and guild composition. (A) Siliciclastic intervals—Q-mode NMDS based on species composition. (B) Siliciclastic intervals—Q-mode NMDS based on guild composition. (C) Carbonate intervals—Q-mode NMDS based on species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

below MSWB are bioturbated and show no signs of high-energy disturbance. The higher proportion of free-lying brachiopods in 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.

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 coexisted 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 and commonly do 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 deposition of the lower part of the Kössen Formation.

Coexistence of Brachiopods with Epifaunal Filibranchs

As follows from Q- and R-mode analyses: (1) brachiopods, as a group, were characterized by a distinct distribution pattern (i.e., brachiopod sample groups do not overlap with bivalve sample groups, and brachiopod species more commonly coexist with other brachiopods than with bivalves), and (2) brachiopod guilds coexisted more commonly with epifaunal than with infaunal and semi-infaunal bivalves. Similar compositional

TABLE 3—Results of ANOSIM tests for 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).

	R Statistic	P-value	Permutations	Number of permuted R \geq observed R
<i>Unit 3-carbonate interval-species</i>				
Above NSWB vs. below NSWB	0.407	0.036	330	12
<i>Unit 3-carbonate intervals-guilds</i>				
Above NSWB vs. below NSWB	0.341	0.061	330	20
<i>Unit 3-siliciclastic interval-species</i>				
Global test	0.706	<0.0001	10000	0
Pairwise 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
<i>Unit 3-siliciclastic intervals-guilds</i>				
Global test	0.641	<0.0001	10000	0
Pairwise comparisons:				
Above NSWB vs. below NSWB	0.694	0.0008	10000	8
Above NSWB vs. below MSWB	0.854	0.0012	792	1
Below NSWB vs. below MSWB	0.3	0.028	2002	57

separation between brachiopods and bivalves was observed in Pennsylvanian–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, because 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 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 habitats that are affected by lower siliciclastic and nutrient supply than 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 also can 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 (typically epifaunal) have higher clearance rates under low particle concentrations, and, thus, are 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. Thus, in contrast to filibranch and pseudolamellibranch bivalves, the metabolic demands of infaunal bivalves may not be fulfilled under nutrient-poor conditions. 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, in contrast to pteriomorph bivalves, decreases markedly towards bathyal and abyssal habitats.

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 mechanisms that minimize energetic ex-

penditure, 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 thus can have similar preferences to filibranch bivalves with respect to the nutrient-supply regime, although they differ in their adaptive strategies (bivalves have higher clearance rates and brachiopods have lower metabolic demands). It should be noted that modern infaunal proto-branchs are able to live in habitats with extreme variations in nutrient supply (Crame, 2002). However, deposit-feeding nuculids only are represented by one rare species in the Kössen Formation, so they do not contribute to the differential distribution of epifauna and infauna.

Furthermore, algal concentrations at which clearance rates decrease or feeding stops are lower in brachiopods than in bivalves (Rhodes and Thompson, 1993). Terebratulid brachiopods stop 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 that usually are much higher than 10,000 cells/ml (Rhodes and Thompson, 1993). This indicates that rhynchonelliformean brachiopods are more vulnerable in habitats with high particle concentrations than bivalves. Thayer (1986) showed that brachiopods possess various pre-ingestion mechanisms that allow them to cope 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 probably is lower in brachiopods than in bivalves. Epifaunal bivalves with heterorhabdic filibranch or pseudolamellibranch gills 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 types, and between bivalves and brachiopods, still is not resolved clearly, 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 potentially can cope with low oxygen concentrations better than eulamellibranch bivalves with lower clearance rates/higher metabolic demands (Childress and Seibel, 1998; Levin, 2003). Brachiopods and filibranch bivalves also can co-occur due to their similar responses to oxygen fluctuations.

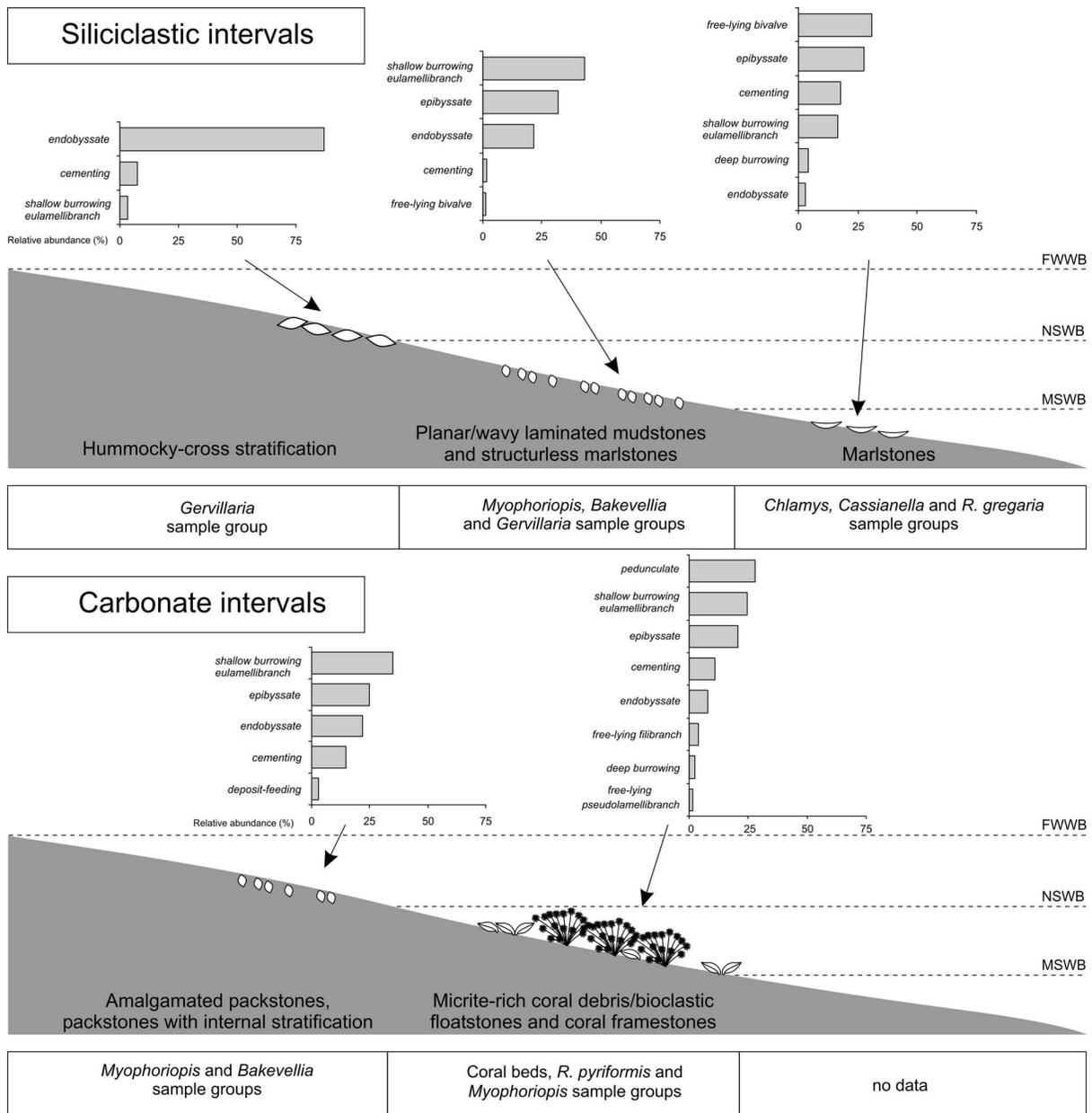


FIGURE 15—Distribution of sample groups along an onshore-offshore gradient in Unit 3. (A) Siliciclastic intervals; note that free-lying bivalves are abundant in deep habitats below MSWB. (B) Carbonate intervals; note that bivalves dominate in shallow habitats and brachiopods in deep habitats.

Dominance of Brachiopods and Epifaunal Bivalves in Soft-Bottom Habitats

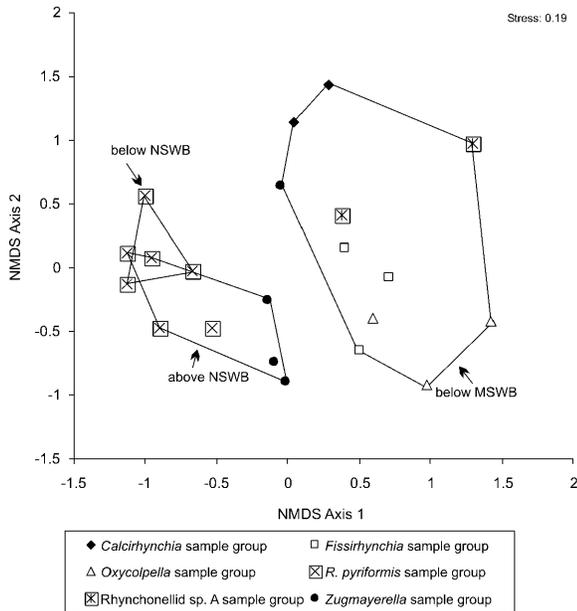
Several hypotheses were proposed in order to explain the absence or rarity of epifaunal, immobile suspension-feeders in present-day soft-bottom habitats, which contrasts with Paleozoic and Mesozoic times when soft-bottom habitats commonly were dominated by poorly mobile epifaunal suspension-feeders (Thayer, 1983; Jablonski and Bottjer, 1983; Holland and Patzkowsky, 2004). In general, it is supposed that a combination of increased biotically induced sediment disturbance and predation during the Mesozoic led to a change in ecology of soft-bottom habitats and to the 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 free-lying and endobysate bivalves and free-lying brachiopods as those guilds that were vulnerable to higher sediment-

mediated disturbance in soft-bottom habitats. Although cementing and epibysate bivalves and pedunculate brachiopods are poorly to non-mobile, they were not included by Thayer (1983) in the category that was vulnerable to sediment-mediated disturbance. This was because these groups mainly were supposed to be inhabitants of hard-bottom habitats. However, these guilds commonly occupy mixed-bottom or soft-bottom habitats, with the possibility of attachment to isolated hard substrates. The increase in sediment disturbance in such habitats also would be disadvantageous for these guilds. Therefore, in this paper, all poorly to non-mobile epifauna, including pedunculate brachiopods, are assumed to have been potential victims of high sediment disturbance rates.

Below, multiple hypotheses explaining the absence of infaunal suspension-feeding bivalves in soft-bottom habitats are evaluated. Because infaunal suspension-feeding bivalves locally are very common in the Kösen Formation, their rarity or absence in soft-bottom habitats should be related to a taphonomic or ecologic explanation. Three soft-bottom

A. Carbonate intervals - species



B. Carbonate intervals - guilds

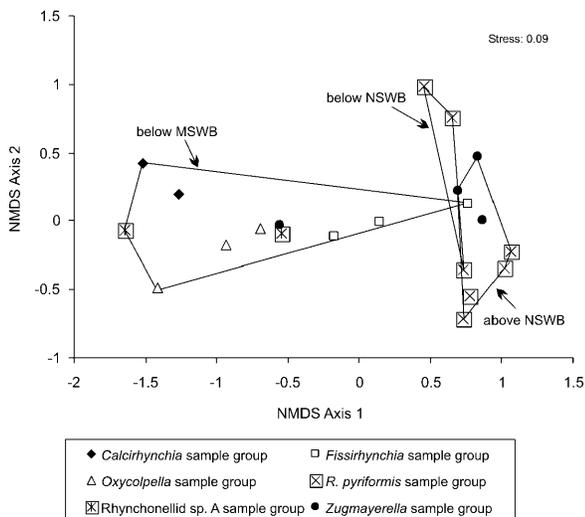


FIGURE 16—Ordination of samples of Unit 4 and Eiberg Member showing between-habitat differences in species and guild composition. (A) Q-mode NMDS based on species composition. (B) Q-mode NMDS based on guild composition.

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 there can be sites for attachment of juvenile brachiopods or bivalves (e.g., shell debris and soft-bodied benthic animals can provide stable support for attachment) in soft-bottom habitats. 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 to Preferential Destruction of Aragonitic Bivalves*: Higher susceptibility of aragonite to dissolution can cause infaunal bivalves to be underrepresented with respect to their community-level abundance because unlike brachiopods and most epifaunal bivalves, which are mainly calcitic, infaunal bivalves are mainly aragonitic

(Jablonski and Bottjer, 1983). This preservation bias can be enhanced by a sampling bias against aragonitic bivalves because molds 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 mostly are preserved as recrystallized shells in marlstones and micrite-rich floatstones of the carbonate and siliciclastic intervals. Internal molds or incompletely dissolved shells are visible locally, but do not prevail in comparison to unaltered shells in thin sections. In addition, marlstones dominated by infaunal and semi-infaunal bivalves lithologically are comparable to marlstones with brachiopods and epifaunal bivalves, indicating that 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 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. Therefore, low abundance of aragonitic bivalves probably reflects the original community composition, and is not a preservation artifact.

(2) *Inhibited Burrowing Ability and Enhanced Substrate Stability*: Firm or shell-rich substrates inhibit penetration by infauna or lead to a decrease in growth rates of infauna, with higher vulnerability to predation or competition as a 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), 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 bottoms 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, and therefore indicate 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 distributions, 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 rates of epifaunal larvae in soft, unstable substrates contrast with inhibited recruitment of larvae of infaunal suspension-feeders. As Jablonski and Bottjer (1983) argued, larvae of infaunal suspension-feeders that 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, 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 may avoid such problems. Because 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 unstable substrate conditions could have been possible for samples dominated by the reclining bivalve *Cassianella*. This bivalve could maintain stable orientation on the sediment-water interface due to its iceberg strategy (Thayer, 1975).

(4) *Inhibited Recruitment of Infaunal Bivalves due to Hypoxia*: Dominance of epifaunal suspension-feeders in soft-bottom habitats also is explained by anoxic conditions at or below the sediment-water interface, excluding deep, and possibly shallow, infaunal mollusks (Oschmann, 1988; Aberhan, 1992). In addition, epifaunal bivalves with high clearance rates and brachiopods with low metabolic demands can cope with oxygen-deficient conditions. Typical epifaunal guilds of Mesozoic

TABLE 4—Results of ANOSIM tests for 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).

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	0.088	364	3
Below NSWB, above NSWB	0.341	0.075	120	9
Below MSWB, above NSWB	0.639	<0.0001	10000	4

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*) went extinct before Rhaetian times, and 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 well-oxygenated bottom waters. 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 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 occupied mainly by epifaunal bivalves or brachiopods. In addition, barren beds in the siliciclastic intervals of the Eiberg Member probably were deposited under dysoxic or anoxic conditions, as indicated by very limited bioturbation, trace-element analyses, and palynofacies (Hüssner et al., 2000; Holstein, 2004). Therefore, the decrease in oxygen

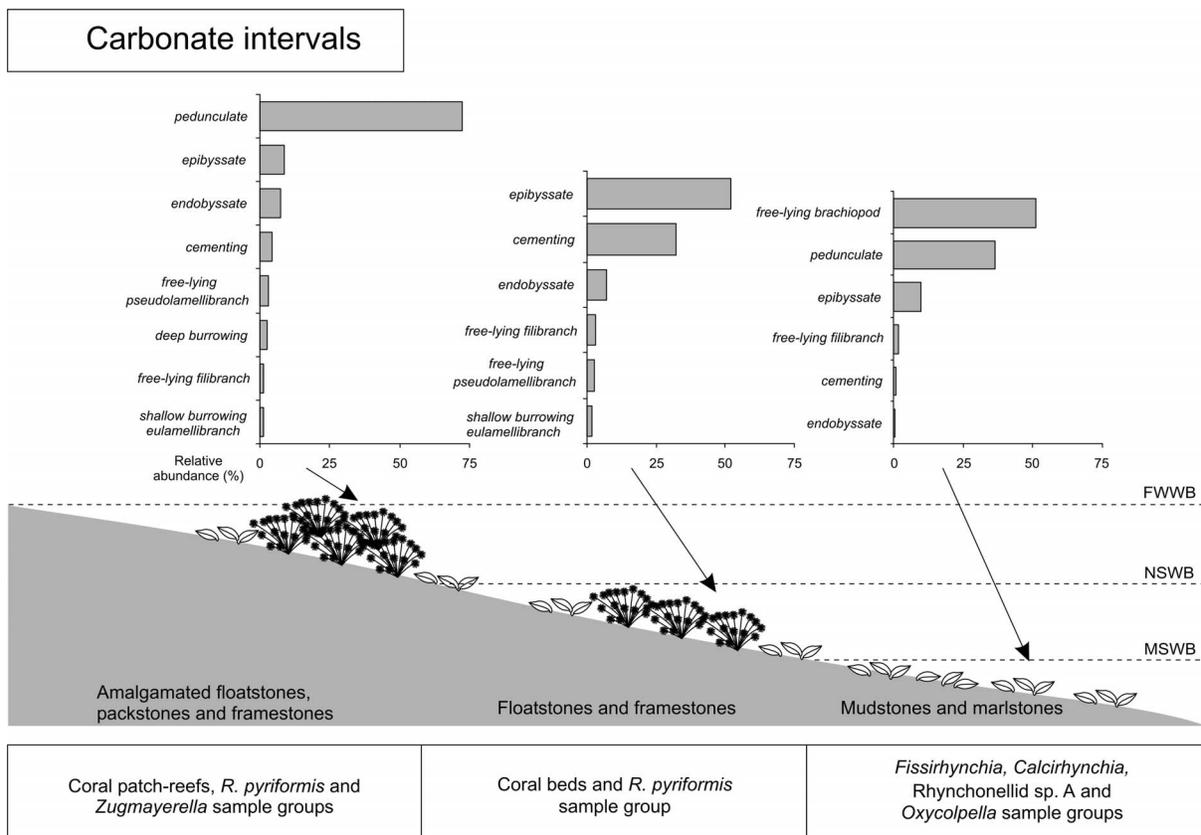


FIGURE 17—Distribution of sample groups along an onshore-offshore gradient in Unit 4 and in the carbonate intervals of the Eiberg Member; note the absence of infaunal bivalves.

concentrations partly can explain the 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 of nutrient-supply control of brachiopod and bivalve communities due to different metabolic demands is not new (Bambach, 1993), its application to soft-bottom habitats was not explicitly stated. 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, actualistic evidence indicates that infaunal (mostly eulamellibranch) and epifaunal (mostly filibranch and pseudolamellibranch) bivalves differ in their feeding strategies with respect to low nutrient supply. During a nutrient-poor carbonate regime, metabolic demands of infaunal suspension-feeding bivalves probably were not fulfilled, and brachiopods and epifaunal bivalves dominated 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 members (Holstein, 2004). Because land-derived nutrient supply decreases in an offshore direction, this argument also can be used to explain the abundance of brachiopods and epifaunal bivalves and the concomitant scarcity of infaunal bivalves in deep, soft-bottom habitats during the nutrient-rich, siliciclastic regimes. An 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 coexistence of guilds and their environmental distribution, although it can be supplemented by a hypothesis concerning varying oxygen levels. For example, a combined effect of varying nutrient supply and oxygen concentrations probably was 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 eutrophic conditions that would be favorable 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.

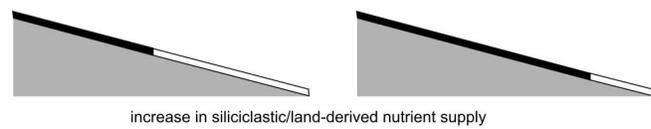
The differential preferences of bivalves and brachiopods with respect to sediment and nutrient supply are supported by several studies. Miller (1988) found that the abundance and diversity of Paleozoic bivalves was substantially greater in siliciclastic than in carbonate habitats. Bambach (1993) suggested that the differential abundance of Paleozoic bivalves in carbonate and siliciclastic environments reflected 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 the Ordovician. Patzkowsky (1995) observed that 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 were dominant and infaunal bivalves were relatively rare in habitats that were 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- and suspension-feeding bivalves.

Onshore-Offshore Expansions and Retreats Related to Siliciclastic Supply

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

(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

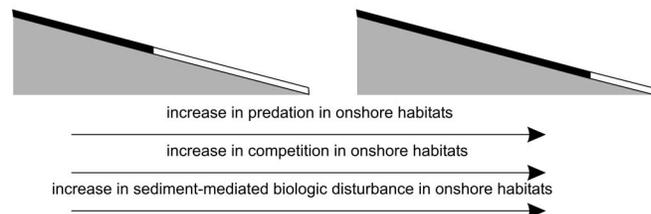
A. Onshore-offshore replacement due to extrinsic cause



— communities dominated by animals with preference to nutrient-rich and high turbidity conditions

— communities dominated by animals with preference to nutrient-poor and low-turbidity conditions

B. Onshore-offshore replacement due to biotic interactions



— communities dominated by animals with high mobility/resistance to predation and competition

— communities dominated by animals with low mobility/resistance to predation and competition

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). (A) In the first case, onshore communities expand because they track increased nutrient supply along an onshore-offshore gradient. (B) In the second case, onshore communities expand into deeper habitats through increased competition ability, higher resistance to predation, or higher resistance to bioturbation.

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 input. 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 low oxygen levels, which also played 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 an 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 thus would lead indirectly to higher bioturbation, which can be detrimental to poorly mobile epifaunal bivalves or brachiopods. The competitive ability of benthic animals with high metabolic demands also would be enhanced under increased nutrient-rich conditions. Although the results presented do not permit evaluation of the role of biotic interactions alone, the onshore-offshore

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 that 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 an offshore direction or by low oxygen levels in the deepest habitats due to restricted circulation.

ACKNOWLEDGMENTS

I thank Michał Kowalewski and Lindsey R. Leighton for detailed and critical reviews, Franz T. Fürsich for comments and discussions, and Peter B. Beninger for several suggestions. All analyses were performed with PRIMER software. The study was supported by the Deutsche Forschungsgemeinschaft (Fu 131/26/1), the Slovak Scientific Grant Agency (6062), and the Ministry of Environment of Slovak Republic (APVV-51-011305), and is a contribution to IGCP 458. This is Paleobiology Database Publication No. 35.

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.
- AGER, D.V., 1965, The adaptation of Mesozoic brachiopods to different environments: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 1, p. 143–172.
- 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.
- ALMÉRAS, Y., and ELMÍ, 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.
- ALROY, J., 2004, Are Sepkoski's evolutionary faunas dynamically coherent?: *Evolutionary Ecology Research*, v. 6, p. 1–32.
- 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.
- 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, Seafloor 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., and 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*: University of Chicago Press, Chicago, p. 123–160.
- 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.
- BARNES, D.K.A., and PECK, L.S., 1997, An Antarctic shelf population of the deep-sea, Pacific brachiopod *Nearhynchia strebeli*: *Journal of the Marine Biological Association of the United Kingdom*, v. 77, p. 399–407.
- BENINGER, P.G., DECOTTIGNIES, P., and RINCÉ, 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.
- BOTTJER, D.J., and JABLONSKI, D., 1988, Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates: *PALAIOS*, v. 3, p. 540–560.
- 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.
- 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.
- 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.
- 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.
- 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., and WARWICK, R. M., 2001, *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, Second Edition: PRIMER-E Ltd, Plymouth, 172 p.
- 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.
- 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., 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.
- 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.
- 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., 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., 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., and WENDT, J., 1977, Biostratigraphy and palaeoecology of the Cassian Formation (Triassic) of the Southern Alps: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 22, p. 257–323.
- 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.
- GARCIA, J.-P., and DROMART, G., 1997, The validity of two biostratigraphic approaches in sequence stratigraphic correlations: brachiopod zones and marker-beds in the Jurassic: *Sedimentary Geology*, v. 114, p. 55–79.
- 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.
- GOLEBIOWSKI, R., 1989, *Stratigraphie und Biofazies der Kössener Formation (Obertrias, Nördliche Kalkalpen)*: Unpublished PhD thesis, University of Vienna, Vienna, 253 p.
- 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.*
- 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.
- 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, Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment: *Marine Ecology-Progress Series*, v. 46, p. 151–165.
- HAAS, J., KOVACS, S., KRYSZYN, 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.

- HARPER, E.M., and SKELTON, P.W., 1993, The Mesozoic Marine Revolution and epifaunal bivalves: *Scripta Geologica*, Special Issue, v. 2, p. 127–153.
- 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.
- HICKMAN, C.S., 1984, Composition, structure, ecology, and evolution of six Cenozoic deep-water mollusk communities: *Journal of Paleontology*, v. 58, p. 1215–1234.
- 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, Zyklustratigraphie und Biomarker in den oberen Kössener Schichten (Alpine Obertrias): *Mitteilungen der Gesellschaft der Geologie- und Bergbaustudenten Österreich*, v. 43, p. 65–66.
- 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.
- 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., 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., GOREAU, T.F., and HARTMAN, W.D., 1971, Recent brachiopod-coraline 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.
- 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.
- 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.
- 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., 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., 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.
- KRUSKAL, J.B., 1964, Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis: *Psychometrika*, v. 29, p. 1–27.
- KUSS, J., 1983, Faziesentwicklung in proximalen Intraplattform-Becken: Sedimentation, Palökologie und Geochemie der Kössener Schichten (Ober-Trias, Nördliche Kalkalpen): *Facies*, v. 9, p. 61–172.
- LABARBERA, M., 1977, Brachiopod orientation to water movement I: 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.
- LAWS, R.A., 1982, Late Triassic depositional environments and molluscan associations from west-central Nevada: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 37, p. 131–148.
- 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., 2004, The K/T event and infaunality: morphological and ecological patterns of extinction and recovery in veneroid bivalves: *Paleobiology*, v. 30, p. 507–521.
- MCCUNE, B., GRACE, J.B., and URBAN, D.L., 2002, Analysis of ecological communities: MjM Software Design, Gleneden Beach, 304 p.
- 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., 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.
- 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.
- MICHALÍK, J., 1977, 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.
- MILLER, A.I., 1988, Spatio-temporal transitions in Paleozoic Bivalvia: an analysis of North American fossil assemblages: *Historical Biology*, v. 1, p. 251–273.
- MINCHIN, P.R., 1987, An evaluation of the relative robustness of techniques for ecological ordination: *Vegetatio*, v. 69, p. 89–107.
- NAVARRO, J.M., LABARTA, U., FERNANDEZ-REIRIZ, M.J., and VELASCO, A., 2003, Feeding behavior and differential absorption 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.
- 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.
- 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.
- Ooi, 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.
- 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.
- OSCHMANN, W., 1988, Upper Kimmeridgian and Portlandian marine macrobenthic associations from southern England and northern France: *Facies*, v. 18, p. 49–82.
- 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.
- 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.
- 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., 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.
- 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.
- 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.
- 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, 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.
- 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.
- 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.
- ROOT, R.B., 1967, The niche exploitation pattern of the blue-gray gnatcatcher: *Ecological Monographs*, v. 37, p. 317–350.
- 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.
- SATTERLEY, A.K., 1996, The interpretation of the Middle and Upper Triassic of the Northern Calcareous Alps: *Earth-Science Reviews*, v. 40, p. 181–207.
- 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., 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*: University of Chicago Press, Chicago, p. 211–255.
- 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 University Press, Princeton, p. 153–190.
- SHI, G.R., 1993, Multivariate data analysis in palaeoecology and palaeobiogeography—a review: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 105, p. 199–234.
- SIBLÍK, M., 1998, A contribution to the brachiopod fauna of the “Oberhätalk” (Northern Calcareous Alps, Tyrol-Salzburg): *Jahrbuch der Geologischen Bundesanstalt*, v. 141, p. 73–95.
- 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.
- SNELGROVE, P.V.R., and BUTMAN, C.A., 1994, Animal-sediment relationships revisited: cause versus effect: *Oceanography and Marine Biology Annual Review*, v. 32, p. 111–177.
- 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.
- 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.
- THAYER, C.W., 1975, Morphologic adaptations of benthic invertebrates to soft substrata: *Journal of Marine Research*, v. 33, p. 177–189.
- 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., 1986, Are brachiopods better than bivalves? Mechanisms of turbidity tolerance and their interaction with feeding in articulated brachiopods: *Paleobiology*, v. 12, p. 161–174.
- 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.
- 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.
- 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 University Press, 527 p.
- 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.
- 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.
- 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.
- WILLAN, R.C., 1981, Soft-bottom assemblages of Paterson Inlet, Stewart Island: *New Zealand Journal of Zoology*, v. 8, p. 229–248.
- WOODIN, S.A., 1976, Adult-larval interactions in dense infaunal assemblages: patterns of abundance: *Journal of Marine Research*, v. 34, p. 25–41.
- 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.

ACCEPTED OCTOBER 25, 2005



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

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

Sample	TH12	TH13-1	GH13-2	TH14	TH15	TH16	TH17	TH18	TH19	TH20	TH21	TH22	TH23
<i>Oxycolpella oxycolpos</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Laballa suessi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sinucostra emmrichi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Zugmayerella uncinata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Zugmayerella koessenensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhaetina gregaria</i>	0	22	56	0	0	0	0	0	0	0	0	0	0
<i>Rhaetina pyriformis</i>	0	0	0	0	0	0	0	0	0	10	0	0	2
<i>Triadithyris gregariaeformis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Zeilleria</i> sp.	0	0	0	0	0	0	0	0	0	0	0	1	7
<i>Austrirhynchia cornigera</i>	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Fissirhynchia fissicostata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calcirhynchia subrimosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhynchonellid</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nuculana claviformis</i>	0	1	0	0	0	0	0	10	4	0	0	0	0
<i>Parallelodon</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Grammatodon</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Inoperna schafhaeutli</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Modiolus minutus</i>	0	0	0	0	0	8	0	0	0	0	0	0	0
<i>Pteria</i> sp. A	0	0	6	0	0	0	0	0	0	0	0	0	0
<i>Rhaetavicula contorta</i>	0	2	25	14	19	0	0	54	8	2	0	1	0
<i>Gervillaria inflata</i>	39	0	0	0	0	14	50	0	5	47	0	0	0

SUPPLEMENTARY DATA 1—Continued.

Sample	TK8	TK9	TK10	TK11	TK12	TG1	TG2	TG3	TG4	TG5	TG6	TG7	TG8
<i>Austrirhynchia cornigera</i>	1	5	0	0	0	0	0	0	0	0	0	0	0
<i>Fissirhynchia fissicostata</i>	0	0	6	0	0	0	0	0	0	0	0	5	7
<i>Calcirhynchia subrimosa</i>	0	15		60	37	0	0	0	0	0	0	0	0
<i>Rhynchonellid</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nuculana claviformis</i>	0	0	0	0	0	0	0	0	3	0	0	0	0
<i>Parallelodon</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Grammatodon</i> sp. A	3	0	0	0	0	0	0	0	0	0	0	0	0
<i>Inoperma schafhaeutli</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Modiolus minutus</i>	7	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pteria</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rhaetavicula contorta</i>	0	0	0	0	0	0	6	174	23	15	0	0	0
<i>Gervillaria inflata</i>	0	0	0	0	0	57	0	2	2	1	17	0	0
<i>Bakevellia praecursor</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cassianella inaequiradiata</i>	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Pinna</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oxytoma inequivalvis</i>	0	2	0	13	8	0	0	0	0	0	0	0	0
<i>Entolium</i> sp. A	0	0	0	1	1	0	0	0	0	0	0	0	0
<i>Propeamussium schafhaeutli</i>	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chlamys coronata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chlamys</i> sp.	4	0	1	3	1	0	2	3	0	1	0	0	0
<i>Atreta intusstriata</i>	5	0	0	0	0	0	37	6	0	0	0	1	2
<i>Placunopsis alpina</i>	1	0	0	0	0	0	0	7	2	1	0	0	0
<i>Antiquilima alpis</i>	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Antiquilima</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Plagiostoma punctatum</i>	5	0	0	0	0	0	0	0	0	0	0	1	2
<i>Liostrea himmities</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Actinostreon haidingerianum</i>	4	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gruenewaldia inflata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Myophoriopsis isoceles</i>	0	0	0	0	0	0	4	16	13	17	0	0	0
<i>Pseudocorbula ewaldi</i>	0	0	0	0	0	0	0	0	0	6	0	0	0
<i>Palaeocardita austriaca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Palaeocardita multiradiata</i>	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Palaeocardita</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protocardia rhaetica</i>	0	0	0	0	0	0	2	0	5	16	0	0	0
<i>Homomya lagenalis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pleuromya</i> sp. A	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Isocyprina alpina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mysidiopora waageni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Schafhaeutlia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Bivalve indet A</i>	0	0	0	0	0	0	0	0	0	0	0	0	1
Sample	TG9	TSA1	TSA2	TSC2	TSC1	TSC4	TSC5	GN24	GHS5				
<i>Oxycolpella oxycolpos</i>	0	0	0	0	0	0	0	0	0				
<i>Laballa suessi</i>	0	0	0	0	0	0	0	0	0				
<i>Sinuocosta emmrichi</i>	0	0	0	0	0	1	0	0	0				
<i>Zugmayerella uncinata</i>	0	0	0	5	11	0	0	0	0				
<i>Zugmayerella koessonensis</i>	0	0	6	0	0	0	7	0	0				
<i>Rhaetina gregaria</i>	0	5	0	15	0	2	0	0	0				
<i>Rhaetina pyriformis</i>	0	7	15	13	0	6	0	0	0				
<i>Triadithyris gregariaeformis</i>	0	0	1	0	0	0	0	0	0				
<i>Zeilleria</i> sp.	5	10	11	14	8	3	3	0	0				
<i>Austrirhynchia cornigera</i>	0	1	7	0	1	1	1	0	0				
<i>Fissirhynchia fissicostata</i>	79	0	7	9	0	0	0	0	0				
<i>Calcirhynchia subrimosa</i>	0	0	0	0	0	0	0	0	0				
<i>Rhynchonellid</i> sp. A	5	0	0	0	0	0	0	0	0				
<i>Nuculana claviformis</i>	0	0	0	0	0	0	0	0	17				
<i>Parallelodon</i> sp. A	0	0	0	0	0	0	0	0	0				
<i>Grammatodon</i> sp. A	0	0	0	0	0	0	0	0	0				
<i>Inoperma schafhaeutli</i>	0	0	0	0	0	0	0	0	0				
<i>Modiolus minutus</i>	0	0	0	2	0	0	0	0	0				
<i>Pteria</i> sp. A	0	0	0	0	0	0	0	0	0				
<i>Rhaetavicula contorta</i>	0	0	0	0	0	0	0	0	0				
<i>Gervillaria inflata</i>	0	1	13	0	0	3	0	82	0				
<i>Bakevellia praecursor</i>	0	0	0	0	0	0	0	0	11				
<i>Cassianella inaequiradiata</i>	0	0	0	0	1	1	0	0	0				
<i>Pinna</i> sp. A	0	0	1	0	0	1	1	0	0				
<i>Oxytoma inequivalvis</i>	10	0	0	0	0	0	1	0	0				
<i>Entolium</i> sp. A	1	0	0	0	0	0	0	0	0				
<i>Propeamussium schafhaeutli</i>	0	0	0	0	0	0	0	0	0				
<i>Chlamys coronata</i>	0	0	0	0	0	0	0	0	0				
<i>Chlamys</i> sp.	7	4	2	1	22	2	0	0	0				

SUPPLEMENTARY DATA 1—Continued.

Sample	TG9	TSA1	TSA2	TSC2	TSC1	TSC4	TSC5	GN24	GHS5
<i>Atreta intusstriata</i>	0	0	1	0	0	0	1	0	0
<i>Placunopsis alpina</i>	0	0	1	1	0	0	0	0	5
<i>Antiquilima alpis</i>	0	0	0	0	0	0	0	0	0
<i>Antiquilima</i> sp. A	0	0	0	0	0	0	0	0	0
<i>Plagiostoma punctatum</i>	0	1	2	1	18	0	0	0	0
<i>Liostrea hinmities</i>	0	0	0	1	2	0	0	8	0
<i>Actinostreon haidingerianum</i>	0	3	1	4	0	1	0	0	0
<i>Gruenewaldia inflata</i>	0	0	0	0	0	0	0	0	0
<i>Myophoriopsis isoceles</i>	0	0	1	0	0	0	0	0	0
<i>Pseudocorbula ewaldi</i>	0	0	0	0	0	0	0	0	0
<i>Palaeocardita austriaca</i>	0	0	0	0	0	0	0	21	0
<i>Palaeocardita multiradiata</i>	0	0	0	0	0	0	0	0	0
<i>Palaeocardita</i> sp. A	0	0	0	0	1	0	0	0	0
<i>Protocardia rhaetica</i>	0	0	0	1	0	0	0	0	0
<i>Homomya lagenalis</i>	0	0	0	0	0	0	0	0	0
<i>Pleuromya</i> sp. A	0	0	1	0	0	1	0	0	0
<i>Isocyprina alpina</i>	0	0	0	0	0	0	0	0	137
<i>Mysidoptera waageni</i>	0	1	1	0	0	0	0	0	0
<i>Schafhaeulia</i> sp.	0	0	0	0	0	0	0	0	0
<i>Bivalve indet A</i>	0	2	0	0	0	0	0	0	0

SUPPLEMENTARY DATA 2—Assignments of samples to stratigraphic units, intervals, and habitats.

Sample	Sample group	Member	Interval	Depth
GH1	<i>Isocyprina</i>	2	siliciclastic	below NSWB
TH2	<i>R. gregaria</i>	2	carbonate	above NSWB
TH3-1	<i>R. gregaria</i>	2	carbonate	above NSWB
TH3-2	<i>R. gregaria</i>	2	carbonate	above NSWB
GH3-3	<i>R. gregaria</i>	2	carbonate	above NSWB
TH4	<i>R. gregaria</i>	2	claystone	below NSWB
TH5	<i>Isocyprina</i>	2	siliciclastic	below NSWB
TH6	<i>Isocyprina</i>	2	siliciclastic	below NSWB
TH7	<i>Isocyprina</i>	2	siliciclastic	below NSWB
GH8	<i>Isocyprina</i>	2	siliciclastic	below NSWB
GH9	<i>Gervillaria</i>	2	siliciclastic	above NSWB
GH10	<i>R. gregaria</i>	2	limestone	above NSWB
TH11	<i>Gervillaria</i>	2	siliciclastic	below NSWB
TH12	<i>Gervillaria</i>	2	siliciclastic	below NSWB
TH13-1	<i>R. gregaria</i>	2	limestone	below NSWB
GH13-2	<i>R. gregaria</i>	2	limestone	below NSWB
TK1	<i>R. gregaria</i>	2	siliciclastic	below NSWB
TK2	<i>Isocyprina</i>	2	siliciclastic	below NSWB
TK3	<i>Isocyprina</i>	2	siliciclastic	below NSWB
GN24	<i>Gervillaria</i>	2	siliciclastic	no data
GHS5	<i>Isocyprina</i>	2	siliciclastic	no data
TH16	<i>Gervillaria</i>	3	siliciclastic	above NSWB
TH14	<i>Bakevella</i>	3	carbonate	above NSWB
TH15	<i>Myophoriopsis</i>	3	siliciclastic	below NSWB
TH17	<i>Gervillaria</i>	3	siliciclastic	above NSWB
TH18	<i>Myophoriopsis</i>	3	carbonate	above NSWB
TH19	<i>Myophoriopsis</i>	3	carbonate	above NSWB
TH20	<i>Gervillaria</i>	3	siliciclastic	below NSWB
TH21	<i>R. pyriformis</i>	3	carbonate	below NSWB
TH22	<i>Cassianella</i>	3	siliciclastic	below NSWB
TE1	<i>Cassianella</i>	3	siliciclastic	below NSWB
TE2	<i>Myophoriopsis</i>	3	carbonate	above NSWB
TE3	<i>Myophoriopsis</i>	3	carbonate	above NSWB
TE4	<i>Myophoriopsis</i>	3	siliciclastic	below NSWB
TE5	<i>Gervillaria</i>	3	siliciclastic	above NSWB
TE6	<i>Gervillaria</i>	3	siliciclastic	above NSWB
TE7	<i>Gervillaria</i>	3	siliciclastic	above NSWB
TE8	<i>Myophoriopsis</i>	3	carbonate	above NSWB
TE9	<i>Myophoriopsis</i>	3	carbonate	above NSWB
TE10	<i>Myophoriopsis</i>	3	siliciclastic	below NSWB
TE11	<i>Myophoriopsis</i>	3	siliciclastic	below NSWB
TE12	<i>Myophoriopsis</i>	3	carbonate	below NSWB
TK4	<i>Bakevella</i>	3	siliciclastic	below NSWB
TK5	<i>Myophoriopsis</i>	3	carbonate	below NSWB
TK6	<i>Chlamys</i>	3	siliciclastic	below NSWB
TK7	<i>Chlamys</i>	3	siliciclastic	below NSWB
TK8	<i>R. pyriformis</i>	3	carbonate	below NSWB
TG1	<i>Gervillaria</i>	3	siliciclastic	above NSWB
TG2	<i>R. gregaria</i>	3	siliciclastic	below NSWB
TG3	<i>Myophoriopsis</i>	3	siliciclastic	below NSWB
TG4	<i>Myophoriopsis</i>	3	siliciclastic	below NSWB
TG5	<i>Myophoriopsis</i>	3	siliciclastic	below NSWB
TG6	<i>Gervillaria</i>	3	siliciclastic	above NSWB
TH23	<i>R. pyriformis</i>	4	carbonate	below NSWB
TE13	<i>R. pyriformis</i>	4	carbonate	below NSWB
TE14	<i>Rhynchonellid A</i>	6–7	carbonate	below MSWB
TE15	<i>Fissirhynchia</i>	6–7	carbonate	below MSWB
TE16	<i>Rhynchonellid A</i>	6–7	carbonate	below MSWB
TE17	<i>Fissirhynchia</i>	6–7	carbonate	below MSWB
TE18	<i>Oxycolpella</i>	6–7	carbonate	below MSWB
TE19	<i>Oxycolpella</i>	6–7	carbonate	below MSWB
TK9	<i>Zugmayerella</i>	6–7	carbonate	below MSWB
TK10	<i>Oxycolpella</i>	6–7	carbonate	below MSWB
TK11	<i>Calcirhynchia</i>	6–7	carbonate	below MSWB
TK12	<i>Calcirhynchia</i>	6–7	carbonate	below MSWB
TG7	<i>Zugmayerella</i>	4	carbonate	above NSWB
TG8	<i>Zugmayerella</i>	4	carbonate	above NSWB
TG9	<i>Fissirhynchia</i>	5	carbonate	below MSWB
TSA1	<i>R. pyriformis</i>	4	carbonate	above NSWB
TSA2	<i>R. pyriformis</i>	4	carbonate	above NSWB
TSC2	<i>R. pyriformis</i>	4	carbonate	above NSWB
TSC1	<i>R. pyriformis</i>	4	carbonate	below NSWB
TSC4	<i>R. pyriformis</i>	4	carbonate	above NSWB
TSC5	<i>Zugmayerella</i>	4	carbonate	above NSWB

SUPPLEMENTARY DATA 3—Assignments of brachiopods and bivalves to guilds.

Taxon	Guild
<i>Oxycolpella oxycolpos</i>	free-lying brachiopod
<i>Laballa suessi</i>	pedunculate brachiopod
<i>Sinuocosta emmrichi</i>	pedunculate brachiopod
<i>Zugmayerella uncinata</i>	pedunculate brachiopod
<i>Zugmayerella koessenensis</i>	pedunculate brachiopod
<i>Rhaetina gregaria</i>	pedunculate brachiopod
<i>Rhaetina pyriformis</i>	pedunculate brachiopod
<i>Triadithyris gregariaeformis</i>	pedunculate brachiopod
<i>Zeilleria</i> sp.	pedunculate brachiopod
<i>Austrirhynchia cornigera</i>	pedunculate brachiopod
<i>Fissirhynchia fissicostata</i>	pedunculate brachiopod
<i>Calcirhynchia subrimosa</i>	free-lying brachiopod
<i>Rhynchonellid</i> sp. A	free-lying brachiopod
<i>Nuculana claviformis</i>	shallow burrowing deposit-feeder
<i>Parallelodon</i> sp. A	epibyssate filibranch
<i>Grammatodon</i> sp. A	epibyssate filibranch
<i>Inoperna schafhaeutli</i>	endobyssate filibranch
<i>Modiolus minutus</i>	endobyssate filibranch
<i>Pteria</i> sp. A	epibyssate filibranch
<i>Rhaetavicula contorta</i>	epibyssate filibranch
<i>Gervillaria inflata</i>	endobyssate filibranch
<i>Bakevella praecursor</i>	endobyssate filibranch
<i>Cassianella inaequiradiata</i>	free-lying brachiopod
<i>Pinna</i> sp. A	endobyssate filibranch
<i>Oxytoma inequivalvis</i>	epibyssate filibranch
<i>Entolium</i> sp. A	free-lying filibranch
<i>Propeamusium schafhaeutli</i>	free-lying brachiopod
<i>Chlamys coronata</i>	epibyssate filibranch
<i>Chlamys</i> sp. A	epibyssate filibranch
<i>Atreta intusstriata</i>	cementing filibranch
<i>Placunopsis alpina</i>	cementing filibranch
<i>Antiquilima alpina</i>	epibyssate filibranch
<i>Antiquilima</i> sp. A	epibyssate filibranch
<i>Plagiostoma punctatum</i>	epibyssate filibranch
<i>Liostrrea himmitis</i>	cementing pseudolamellibranch
<i>Actinostreon haidingerianum</i>	free-lying pseudolamellibranch
<i>Gruenewaldia inflata</i>	shallow burrowing filibranch
<i>Myophoriopsis isocles</i>	shallow burrowing eulamellibranch
<i>Pseudocorbula ewaldi</i>	shallow burrowing eulamellibranch
<i>Palaeocardita austriaca</i>	shallow burrowing eulamellibranch
<i>Palaeocardita multiradiata</i>	shallow burrowing eulamellibranch
<i>Palaeocardita</i> sp. A	shallow burrowing eulamellibranch
<i>Protocardita rhaetica</i>	shallow burrowing eulamellibranch
<i>Homomya lagenalis</i>	deep burrowing eulamellibranch
<i>Pleuromya</i> sp. A	deep burrowing eulamellibranch
<i>Isocyprina alpina</i>	shallow burrowing eulamellibranch
<i>Mysidoptera waageni</i>	epibyssate filibranch
<i>Schafhaeutlia</i> sp.	shallow burrowing eulamellibranch
Large bivalve A	deep burrowing eulamellibranch