

Testing the role of biological interactions in the evolution of mid-Mesozoic marine benthic ecosystems

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Abstract.—Evaluating the relative importance of biotic versus abiotic factors in governing macroevolutionary patterns is a central question of paleobiology. Here, we analyzed patterns of changes in global relative abundances and diversity of ecological groups to infer the role of biological interactions as driving evolutionary forces in mid-Mesozoic macrobenthic marine ecosystems. Specifically, we tested the hypothesis of escalation, which states that macroevolutionary patterns were controlled by an increasing pressure exerted by enemies on their victims. Associated with evidence of increasing levels of predation and biogenic sediment reworking (bulldozing) is an increasing representation of predation- and disturbance-resistant groups in the fossil record. In particular, we observe increasing proportions of mobile organisms; a decline of vulnerable epifauna living freely on the substrate; and a trend toward infaunalization of the benthos. These trends were most pronounced in the paleotropics, i.e., the region where biological activity is thought to have been highest. The observation that these changes affected several biotic traits and occurred within independent clades argues against the overriding role of a single key adaptive innovation in causing shifts in ecological abundance. Also, changes in the abiotic environment cannot explain these faunal patterns because of lacking cross-correlations with physico-chemical parameters such as global sea level, climate, and seawater chemistry. We conclude that in marine benthic ecosystems of the mid Mesozoic, enemy-driven evolution, or escalation, was a plausible and important factor.

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Introduction

Although the ecological importance of biotic interactions such as predation and competition is widely recognized, their role in determining macroevolutionary trends remains controversial (e.g., Miller 1998). The middle to late Mesozoic was identified as a time in earth history during which predation increased substantially and characteristics that enhance resistance against shell-breaking taxa became more common, a phenomenon that has been referred to as the Mesozoic Marine Revolution (Vermeij 1977, 1987). This was also a time when biological disturbance of marine sediments, or bioturbation, was most pronounced (Thayer 1983). If natural selection due to these biological factors was evolutionarily important, we anticipate that functional groups that were less affected by predators and biological reworking of sediment should have increased with time, whereas vulnerable groups should not. Herein we (1) briefly summarize the evidence of increasing predation and biogenic

mixing of sediment in mid-Mesozoic time; (2) formulate predictions about how these changes should have affected patterns of diversity and ecological abundance in Jurassic marine communities; (3) analyze quantitative changes in the representation of ecological categories, i.e., various life habits, feeding modes, and the mobility of benthic macroinvertebrates; and (4) discuss to what extent emerging trends may reflect intensified biotic interactions.

Database and Methods

Our analysis differs from previous ones by including diversity and abundance information from all well-represented benthic invertebrate groups (i.e., bivalves, gastropods, brachiopods, echinoids, corals, and sponges) at a global scale and at a relatively fine temporal resolution. Our data are deposited in the Paleobiology Database (PBDB) and are available online (<http://paleodb.org>). The raw data, as of 19 December 2004, comprise more than

TABLE 1. Geographic coverage of the data based on taxonomic occurrences of benthic invertebrate species.

| Regions/Time | Europe | North America | South America | Africa and India | Asia incl. Russia |
|-----------------|--------|---------------|---------------|------------------|-------------------|
| Early Jurassic | 57% | 2% | 38% | 2% | 2% |
| Middle Jurassic | 41% | 2% | 2% | 33% | 23% |
| Late Jurassic | 90% | <1% | <1% | 7% | 3% |

2800 Jurassic non-reef macrobenthic collections (faunal lists), with more than 22,000 taxonomic occurrences. Much of the information comes from quantitative bed-by-bed sampling of level-bottom paleocommunities done by the authors. The analyses were performed at the stage level. Absolute ages for Jurassic stage boundaries are still poorly constrained, but following Gradstein and Ogg (2004) the duration of Jurassic stages ranges from 3.1 Myr (Hettangian) to 7.4 Myr (Toarcian) with an average duration of 4.9 Myr. To achieve a high reliability of global ecological proportion estimates, a minimum of 1000 occurrences per time interval were used, which required combining the Aalenian and Bajocian stages (7.9 Myr).

The geographic coverage (Table 1) is not even (and never will be, because of geographic variation in outcrop area). Early Jurassic data are primarily from Europe and South America, whereas North America, Africa, and Asia only account for little more than 5% of the occurrences. In the Middle Jurassic, the data are more evenly distributed between Europe, Africa, and Asia. The vast majority of Late Jurassic occurrences are from Europe, with extra-European regions contributing only 10% to the data. It should be kept in mind, however, that Europe yields a wide variety of Jurassic environments and paleolatitudinal zones, extending from present-day Portugal and Sicily up to Greenland.

We assume that the sum of changes at the local and regional level is a fair representation of the global picture. Bambach (2002: p. 319) argued that “global analyses may not reveal the detailed story of changes in organism-organism interactions in each local setting, but global analyses provide invaluable indices of when local changes must have been occurring.” This conclusion may be questioned if systematic sampling biases exist. For example, if cold-water communities were overrepre-

sented at one time compared with another, a spurious pattern might emerge reflecting only the distribution of samples (see also Vermeij and Leighton 2003). To account for such sampling artifacts in our global analysis, we therefore distinguished between the following large-scale environments: low paleolatitudes versus mid to high paleolatitudes (with a cut-off at 35° N and S); carbonates versus siliciclastics (with mixed lithologies assigned to carbonates); shallow-water (above storm wave base) versus deeper-water (below storm wave base) habitats; and combinations thereof. The data were extensively checked for possible synonymies based on the taxonomic experience of the authors. We also categorized taxa ecologically in terms of life habit, feeding strategy, locomotion, and the way stability was attained on the seafloor (see Table 2 for a complete list of ecological/morphological categories). Calculations of the relative abundance of ecological groups are based on species-level data; genera lacking species identifications were included if ecological assignments could be performed unambiguously. Bivalve and gastropod species were also scored for the degree of ornamentation (Table 2). To assess ornamentation quantitatively, taxa with a smooth shell were scored as 1, those with a moderately strong ornament as 2, and those with a strong ornament (e.g., with coarse ribs, spines, knobs) as 3. Size was estimated by the geometric mean of height and length of the largest known specimen of each bivalve species. Measurement of maximum size and categorization of ornament were greatly aided by the Jurassic bivalve catalog, housed at the Department of Earth and Environmental Sciences, Munich. This catalog contains photocopies of approximately 90% of all figured specimens of Jurassic bivalves.

We measured abundances as the number of occurrences of a taxon rather than the cumulative number of specimens or individuals in

TABLE 2. Ecological categorization of mid-Mesozoic benthic macroinvertebrates. Where allocation into one category was impossible, as was the case for many gastropods whose feeding strategy could have been "detritivore/omnivore" or "herbivore", species were assigned to both categories. "Carnivore" comprises scavengers and predators, but excludes microcarnivores such as corals.

| Ecological trait | Category |
|------------------------|--|
| Life habit | Epifaunal |
| | Semi-infaunal |
| | Shallow infaunal |
| | Deep infaunal |
| Feeding strategy | Suspension feeder |
| | Within-sediment deposit feeder |
| | Surface deposit feeder |
| | Detritivore/omnivore |
| | Herbivore |
| | Carnivore |
| | Microcarnivore |
| | Microcarnivore and photosymbiont |
| | Mucus tube-feeder and/or chemosymbiont |
| Locomotion | Sessile |
| | Facultatively mobile |
| | Mobile |
| Means of stabilization | By weight or shape (free-living) |
| | Epibyssate |
| | Endobyssate |
| | Cemented |
| | Endolithic |
| | Pedunculate |
| Ornamentation | With roots |
| | Shell smooth |
| | Moderately ornamented |
| | Strongly ornamented |

individual collections. That the number of taxonomic occurrences can be used as a surrogate of abundance has been previously demonstrated (Hayek and Buzas 1997). Diversity was calculated at the species level. We focus here on changing proportions of ecological groups to diversity and abundance patterns rather than on absolute values. By doing so, potential artifacts related to variations in sampling intensity are minimized. The statistical significance of ecological trends was assessed by a rank-order correlation of logit-transformed proportional data against time (see figure captions). We calculated 95% confidence binomial errors for each category. To provide an indication of the reliability of the data, error bars are commonly shown for one category. Additional error bars were not included in the figures to avoid obscuring of the histograms. Finally, we tested for cross-cor-

relations of detrended data between biotic traits and various abiotic factors based on literature data, which were averaged to correspond to our stratigraphic intervals.

Evidence of Predation in the Mid Mesozoic

To argue plausibly for a causal link between intensified biotic interactions and the adaptive response of organisms it is essential to demonstrate temporal coincidence between the onset (and intensity) of the presumed selective agents and concomitant changes in defensive adaptations.

In the case of predation, two principal types of information can be used to infer its importance in mid-Mesozoic time. These are (1) estimates of the diversity and abundance of predators; and (2) a quantitative appraisal of the traces of predation such as breakage, drilling, or repair of shells. It should be noted that some methods of predation, for example whole-organism ingestion or the nipping of bivalve siphons by fish or crabs, leave no signature on the prey's hard parts. As a result, predation pressure may have existed but remains unrecognized in the fossil record.

Using Sepkoski's compendium of fossil marine animal genera (Sepkoski 2002), Bambach (2002) estimated the global diversity of marine predators through the Phanerozoic. According to his synthesis, the Jurassic was marked by a gradual, approximately three- to fourfold increase in generic diversity of predators, which, however, is not evenly distributed across all predator groups. Anthozoans, polychaetes, and Mesozoic cephalopods generally are not regarded as predators of hard-shelled macrobenthos, i.e., the group of organisms we analyze herein, and therefore are not considered further. In the case of Jurassic ammonites, for example, the few specimens with stomach contents suggest that most of their prey was plankton and nekton (Jager and Fraaye 1997). An exception may be the Octopoda, which possibly range back to the Middle Jurassic, but it is unclear when the drilling habit evolved in this group.

With respect to other predator groups, the number of predaceous gastropod genera tripled during the Jurassic, mainly due to the diversification of the Opisthobranchia (Bambach

2002). An even more prominent diversity rise characterized predatory marine arthropods (Bambach 2002). Homarid and palinurid lobsters evolved in the Triassic, and the Jurassic and Early Cretaceous saw the rise of malacostracan crustaceans with crushing chelae. Echinoderms exhibit the steepest diversity increase of all groups from virtually no records in the Late Triassic to a minimum standing diversity of 17 predatory genera in the Late Jurassic (Bambach 2002). Ophiuroids and echinoids contributed only little to this pattern, and the majority of predatory echinoderms were asteroid starfish. Although diversification of modern-type asteroids was underway during the Triassic (Blake and Hagdorn 2003), their major adaptive radiation occurred during the Jurassic (e.g., Donovan and Gale 1990). For example, the family Asteroiidae, which contains the only living starfish capable of pulling apart the valves of bivalves and brachiopods, apparently originated in the Pliensbachian. Finally, marine vertebrate predators show a moderate increase in diversity, with fishes being the group with the highest diversity. Within the Chondrichthyes, modern-type bottom-dwelling, shell-crushing neoselachian sharks and rays diversified and increased in abundance during the Jurassic, and within the Osteichthyes the same is true of the pycnodonts and teleosts (J. Kriwet personal communication 2004). Direct evidence, such as gastric residues, testifies to the shell-breaking feeding habits of these groups. The Triassic to Early Cretaceous diversity of marine predatory reptiles was relatively low and fluctuated without a consistent trend. Jurassic predatory marine reptiles include ichthyosaurs, plesiosaurs, and pliosaurs, but they seem to have fed mainly on pelagic rather than benthic prey (e.g., see review by Walker and Brett 2002).

Independent evidence of the importance of predation as a selective force comes from the record of drilling and repaired shell injuries (e.g., Kelley and Hansen 2003; Alexander and Dietl 2003). Drilling behavior in gastropods is known since the Paleozoic, but the primary predatory drillers of modern molluscs did not begin to diversify until the Cretaceous. Nevertheless, drill holes in bivalves that are reminiscent of those produced by naticid and

muricid gastropods were reported from the Upper Triassic (e.g., Fürsich and Jablonski 1984) and Lower Jurassic (Harper et al. 1998) respectively. Although the producers of these boreholes remain unknown, Harper et al. (1998) suggested that, at least locally, levels of boring predation in Pliensbachian bivalves were as high as those recorded in many Recent malacofaunas. In contrast, Kowalewski et al. (1998) concluded that drilling predation in Jurassic bivalves and brachiopods occurred only rarely, albeit continuously, and may have had little impact on benthic marine communities. Similarly, Harper and Wharton (2000) documented the continuous presence of predatory boreholes in Jurassic articulate brachiopods from northwest Europe, but the numbers of bored specimens are generally low. With respect to repaired injuries, the frequency of shell repair in gastropods increased between the Late Triassic and Late Cretaceous (Vermeij et al. 1981; Vermeij 1987), although it is unclear exactly when this increase took place. In contrast to gastropods, a preliminary analysis of bivalved animals failed to reveal any trend in the abundance of repaired injuries over time (Vermeij 1987). Finally, Kröger (2000) documented sublethal injuries in Jurassic ammonoids, including examples of benthic crustaceans preying on nektonic ammonoids.

In summary, the history of injuries in benthic prey provides some support for elevated predation pressure in the mid Mesozoic. Also, this interval was characterized by a gradual but distinct increase in predator diversity, albeit moderate compared with Late Cretaceous and Cenozoic levels (see Bambach 2002). Accordingly, if predation played a role in the evolution of mid-Mesozoic benthic invertebrates one would expect moderate and continuous trends in prey morphology and behavior rather than strong and sudden antipredatory responses, unless the studied biotic systems are characterized by threshold effects and non-linearities.

Evidence of Bioturbation in the Mid-Mesozoic

The movement, feeding, and respiration activities of infaunal animals modify marine sediments in many ways. Bioturbation in-

creases the oxygen concentrations within the sediment, which, in turn, affects the biomass of the infauna, the rate of organic matter decomposition, and the recycling of nutrients essential for primary productivity (e.g., Solan et al. 2004). It has, however, negative consequences for sessile or relatively immobile organisms (e.g., see reviews in McCall and Tevesz 1982; Thayer 1983). For example, the displacement and manipulation of sediment during burrowing and feeding may result in the exhumation, burial, and/or disorientation of other animals. Sediment-feeders "mine" the sediment by ingestion and egestion and thus produce two disturbances that often occur at different places. Resuspension of fine bottom sediment can be another consequence of deposit feeding with adverse clogging effects on the filter apparatus of suspension feeders ("trophic group amensalism" [Rhoads and Young 1970]). In the Recent, examples of the exclusion of taxa by bioturbation in unconsolidated marine sediments can be found in a variety of trophic types and in a variety of substrates ranging from mud to sand and even gravel (Thayer 1983: Table IV). Thayer (1983) produced a comprehensive review of the Phanerozoic history of sediment-mediated biological interactions. He adopted a strongly actualistic approach by recording the times of first appearance of modern bioturbators in the Phanerozoic and by assuming that their intensity of bioturbation has remained constant over geologic time. Plotting various measures of biologic reworking of extant taxa as a function of their time of origin in the fossil record led him to conclude that post-Paleozoic taxa rework sediment faster, feed deeper, and have higher sediment turnover rates than Paleozoic taxa. His data show a distinct increase in bioturbation during the Jurassic. In fact, this period saw the most substantial increase for the entire Phanerozoic in the number of classes with intensively bioturbating members (defined as reworking the sediment at a per capita rate of 10 cm³ per day or higher) and the number of classes with deeply bioturbating members (defined as burrowing to a depth of 10 cm or more) (Vermeij 1987: Fig. 5.1). Important bioturbators that first appeared and/or radiated in the Late Triassic or Jurassic in-

clude irregular sea urchins, astropectinid starfish, thalassinidean decapod crustaceans, infaunal gastropods, heterodont bivalves, rays, and possibly also lugworms.

Further evidence of increasing bioturbation intensities comes from an analysis of secular changes in the nature of bedding and storm stratification. Generally, in Mesozoic and Cenozoic sediments biogenic homogenization is much more common and fine bedding is much more limited than in Paleozoic sediments, and the frequency of discrete storm beds decreased substantially from the Mesozoic onward, apparently because of increased destruction of tempestites by subsequent bioturbation (Sepkoski et al. 1991). Brandt (1986) recorded an increase in the minimum bedding thickness of tempestites from a pre-Jurassic value of 1 cm to a value of 3 cm in the Jurassic and correlated this observation with an increase in mean reworking depth of infaunal organisms. Studies of burrows also reveal that their "average maximum" penetration depth increased from 10–20 cm in the Paleozoic to 100–150 cm in Permian to Early Jurassic times (Kidwell and Brenchley 1996 and references therein).

Biotic Interactions and Expected Trends in Mid-Mesozoic Macrobenthos

The observed increase in predation intensity and bioturbation over the Phanerozoic formed the basis for an important macroecological hypothesis, Vermeij's (1987) hypothesis of escalation. The hypothesis of escalation states that over geological time biological hazards such as predation and competition have increased and so have taxa with morphological or behavioral attributes better suited to these changing environmental conditions. Given the rise of predators during the mid Mesozoic (see above), we would expect an increasing representation of highly escalated taxa over this time interval, that is, taxa with characteristics that enhance resistance against, or escape from, shell-breaking taxa. The hypothesis of escalation also includes Thayer's (1979, 1983) bulldozing hypothesis, which claims that the biological disturbance of marine sediments has increased during the Phanerozoic. Given the record of mid-Meso-

TABLE 3. Expected trends in biological traits resulting from increasing predation and bulldozing. Upward- and downward-directed arrows indicate a proportional increase and decrease, respectively, of a biological trait. Double arrow: Result agrees with expectation. Single arrow: Result does not correspond to expected trend.

| | Predation | Bulldozing |
|------------------------|-----------|------------|
| Mobility | ↗ | ↗ |
| Free-living life habit | ↘ | ↘ |
| Cemented vs. byssate | ↗ | |
| Infaunalization | ↗ | ↗ |
| Size of epifauna | ↗ | ↗ |
| Ornamentation | ↗ | |
| Suspension feeding | | ↘ |

zoic bioturbation (see above) this results in the general expectation that the importance of functional groups that are immune to bioturbation should increase, whereas vulnerable groups should decline.

In the following, we specify certain predictable consequences that result from the escalation hypothesis and that can be tested with our data of Mesozoic marine invertebrates. We focus on two aspects of escalation, predation and bioturbation. In an attempt to disentangle their relative importance we formulate predictions separately for both aspects of escalation. As will be seen, however, the predictions for both ecological processes overlap strongly (Table 3):

1. The abundance and diversity of mobile animals should increase under both scenarios, increasing predation and increasing bioturbation. In the case of predation this would represent an escape strategy. For example, many bivalves employ locomotion as the principal mode of antipredatory defense, either by the ability to swim, as in some pectinids and limids, or by rapid burrowing as in many heterodonts. Mobility also enables benthic animals to reoccupy a favorable growth position following disturbance by bioturbation.
2. For the same reasons that overall mobility should increase, the relative abundance of sedentary free-living forms on unconsolidated substrates should decrease under the influence of both predation and bioturbation.
3. Experimental evidence suggests that in bivalves cementation affords better protec-

- tion against predators than the byssate life habit because cementation hampers the manipulation of the bivalve by the predator (Harper 1991). Accordingly, starting with the massive appearance of the cemented habit in the Late Triassic and Early Jurassic (Hautmann 2001, 2004), the abundance and diversity of cemented bivalves should increase relative to byssate bivalves.
4. Infaunal habitats should be increasingly colonized because they are out of the reach of surface-dwelling predators and, in the case of bioturbation, because the mobility of free-burrowing taxa makes them largely immune to bioturbation.
 5. Large size of the epifauna is considered an antipredatory strategy and also provides an insurance against the adverse effects of biologically produced disturbance of sediment. Therefore, the proportion of large epifaunal shells should have increased over time.
 6. A strong sculpture is another characteristic feature that enhances resistance against shell-breaking taxa, and strongly ornamented epibenthos should become more abundant accordingly. However, strong sculpture does not seem to be an adaptive improvement against disturbance by bioturbation, and no trend is expected in this case.
 7. Finally, resuspension of bottom sediment could lead to clogging of the filter apparatus of suspension feeders. This trophic group should therefore be adversely affected by more intense bioturbation, whereas predation does not seem to systematically favor or discriminate against any particular feeding strategy.
 8. In modern oceans, the intensity of predation and bioturbation is higher in the tropics as compared with temperate zones (Vermeij 1987). This latitudinal gradient also appears to have existed in the geological past (e.g., Leighton 1999). Therefore, if predation and bulldozing had substantial influence on the structure of mid-Mesozoic shelf ecosystems, the expectations outlined above should be particularly well expressed in low paleolatitudes.

Results

To evaluate the existence of any directional trends in the various biotic traits outlined above, we calculated their proportional species diversity (Fig. 1) and proportion of occurrences (our surrogate for abundance) (Figs. 2–9). As a rule, for each specific set of data, both measures covary tightly and show essentially the same patterns.

Mobility

In agreement with our prediction, the overall mobility of benthic macroinvertebrates increased over the studied time interval (Figs. 1A, 2A). This pattern is most clearly developed in warm shallow waters of low latitudes (Fig. 2B). It holds true for highly mobile taxa and is even more pronounced in those taxa categorized as facultatively mobile. The latter group includes shallow infaunal suspension-feeding bivalves as the major contributors. To investigate whether the observed trend toward elevated levels of mobility is solely due to intensified colonization of the infaunal habitat, we analyzed the epifauna separately. The trend of increasing Jurassic mobility is no longer evident at the global scale (Fig. 2C) but remains in low latitudes, shallow-water environments, carbonate settings, and combinations thereof (e.g., Fig. 2D). In fact, in these habitats the proportion of the facultatively mobile group, i.e., entoliid, propeamussiid, and pectinid bivalves capable of swimming, declined. However, this is more than compensated for by an increase in the proportional abundance and diversity of highly mobile epifauna, which comprises vagile gastropods and regular echinoids.

Free-living Life Habit

Similarly, our second expectation is met: The guild of sedentary, free-living suspension feeders was moderately well represented in pre-Bathonian times, whereas it played a numerically negligible role in the later part of the Jurassic (Figs. 1A, 3). Apart from a few occurrences of relatively small solitary scleractinian corals, all sedentary free-living forms are bivalves. Most important are various gryphaeid oysters, the large limid *Ctenostreon*, the neith-eid *Weyla*, and the posidoniid *Bositra*.

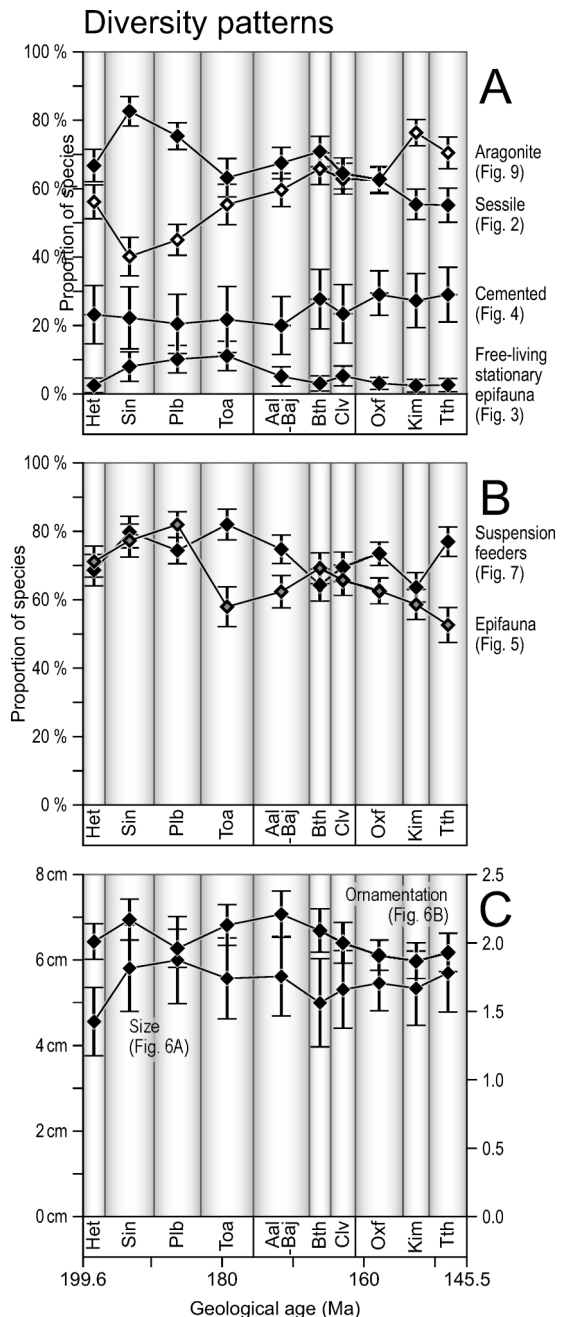


FIGURE 1. Trends in ecological, morphological, and mineralogical traits in Jurassic level-bottom communities based on the number of invertebrate species. Reference to figures showing the trends for occurrences are given in brackets. In C, left-hand scale refers to mean size and right hand scale refers to mean ornamentation. Abbreviations of time intervals: Het = Hettangian; Sin = Sinemurian; Plb = Pliensbachian; Toa = Toarcian; Aal-Baj = Aalenian to Bajocian; Bth = Bathonian; Clv = Callovian; Oxf = Oxfordian; Kim = Kimmeridgian; Tth = Tithonian. Timescale based on Gradstein and Ogg (2004). Error bars represent 95% confidence intervals.

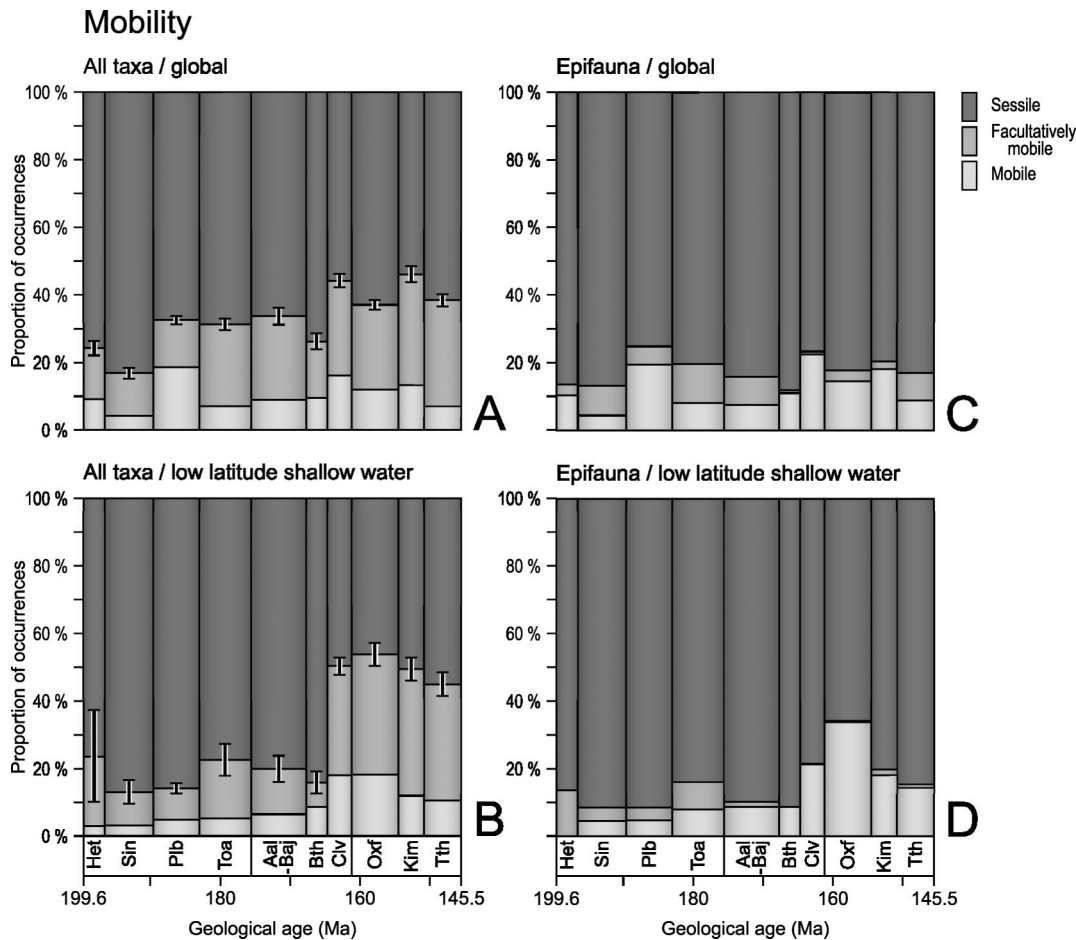


FIGURE 2. Proportion of sessile, facultatively mobile, and highly mobile species (bivalves, gastropods, brachiopods, echinoids, and non-reef corals and sponges) based on taxonomic occurrences in Jurassic level-bottom communities. Sessility on a global scale (A) significantly decreased during the Jurassic (Spearman's rank $r_s = 0.82$, $p = 0.004$). This is also true when only low latitude shallow-water faunas are analyzed (B) ($r_s = 0.70$, $p = 0.03$). When only epifaunal taxa are considered, global sessility (C) lacks a significant trend ($r_s = 0.38$, $p = 0.28$), but declining sessility of epifauna in low-latitude shallow waters (D) is still weakly significant ($r_s = 0.62$, $p = 0.05$). Error bars for facultatively mobile occurrences represent 95% confidence intervals.

Cemented versus Byssate Life Habit in Bivalves

Within fixosessile bivalves, epibyssate forms were more abundant and diverse than those cemented to hard substrates throughout the Jurassic (Figs. 1A, 4). The predominant cementing taxa are various groups of oysters, members of the Plicatulidae and the genus *Placunopsis*, whereas the wide spectrum of byssate taxa has representatives in the bivalve orders Pterioidea (e.g., *Plagiostoma*, *Chlamys*, *Camptonectes*, *Oxytoma*), Mytiloidea (e.g., *Modiolus*), and Arcoidea (e.g., *Grammatodon*). However, in neither of the environmental categories

is there any significant increase of cemented forms relative to epibyssate bivalves, so our expectation is not fulfilled.

Infaunalization

We identify the Jurassic as an important period of infaunalization (Figs. 1B, 5). The more than twofold rise in the proportion of infaunal occurrences is due principally to shallow infaunal burrowers. This group includes a variety of higher taxa, by far the most important of which are suspension-feeding heterodont bivalves (e.g., numerous genera of the families Astartidae, Arcticiidae, and Cardiidae). These

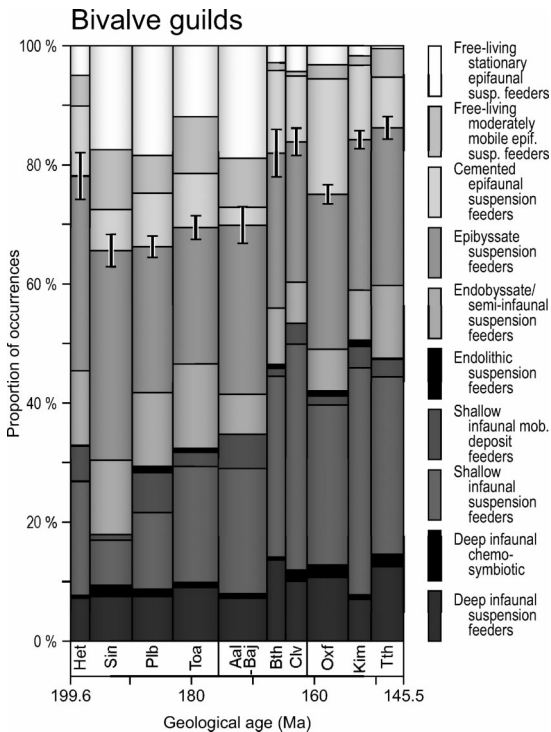


FIGURE 3. Proportion of ecological guilds of bivalves in Jurassic level-bottom communities based on taxonomic occurrences. The relative importance of species with a free-living stationary life habit declined during the Jurassic ($r_s = 0.77$, $p = 0.009$). Error bars for occurrences of epibyssate suspension feeders represent 95% confidence intervals. For legend see Figure 1.

are followed by trigoniid bivalves and deposit-feeding nuculoid bivalves. Other shallow infaunal groups are represented by deposit-feeding (e.g., *Nerinea*) and suspension-feeding gastropods and deposit-feeding irregular echinoids (e.g., *Nucleolites*). Inarticulate brachiopods are of very minor importance. The share of deep infauna, by contrast, rose only slightly during the Jurassic. This ecological group comprises bivalves with one of two trophic strategies, the mucus tube-feeding and/or chemosymbiotic lucinids and the suspension-feeding Pholadomyiidae (e.g., *Pleuromya*, *Pholadomya*) and Tancrediidae. Semi-infaunal bivalves remained rare, without consistent trends throughout the Jurassic. Altogether, the overall representation of the epifauna declined from ~75% in the earliest Jurassic to ~50% in the latest Jurassic. The increase of shallow infauna relative to epifauna is manifested in all our environmental categories, and

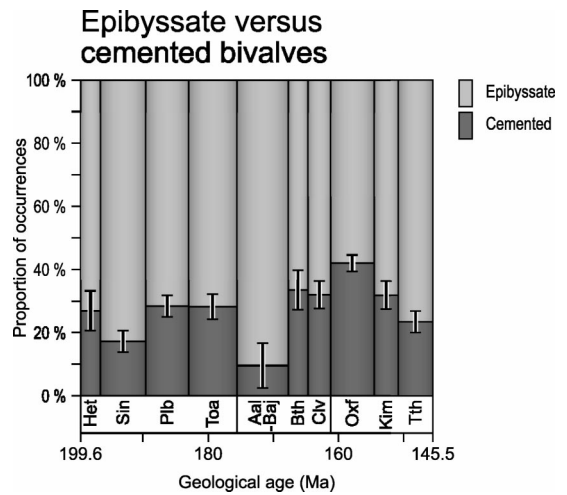


FIGURE 4. Proportion of epibyssate versus cemented Jurassic bivalves based on taxonomic occurrences. There is no significant increase of cemented taxa during the Jurassic ($r_s = -0.39$, $p = 0.27$). Error bars for cemented bivalves represent 95% confidence intervals. For legend see Figure 1.

is most markedly expressed in low latitudes and shallow-water environments. In contrast, the modest increase of deep burrowing bivalves is only evident in mid to high latitudes and in offshore settings.

Size

We tested the prediction that the representation of large epifaunal shells should increase

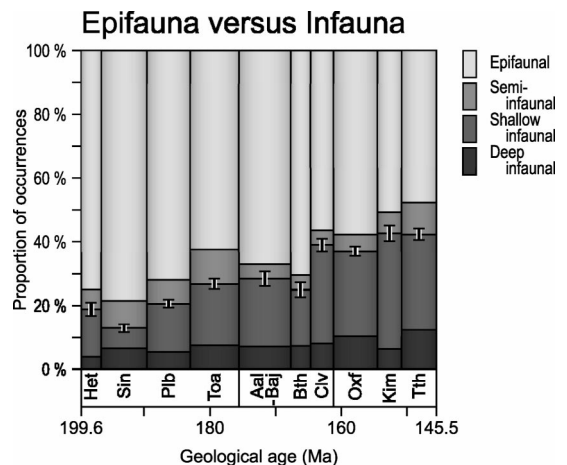


FIGURE 5. Proportion of epifaunal, semi-infaunal, shallow infaunal, and deep infaunal taxa in Jurassic level-bottom communities based on taxonomic occurrences. The proportion of epifaunal organisms significantly decreased during the Jurassic ($r_s = 0.89$, $p = 0.001$). Error bars for shallow infaunal occurrences represent 95% confidence intervals. For legend see Figure 1.

over the studied time interval by using bivalves, for which appropriate data could be obtained from the bivalve catalog (see methods). The mean size of the epifauna, expressed as the average geometric mean of shell length and shell height, fluctuates around 5 cm for most of the Jurassic, but was distinctly larger for the Sinemurian and Pliensbachian (Fig. 6A). This peak is partly due to abundant occurrences of large-sized pectinoids in South America, in particular various species of the genus *Weyla*. But even if *Weyla* is removed from the data, the peak remains, albeit somewhat less pronounced. The Aalenian–Bajocian minimum in mean size is due to a large number of occurrences from the early Aalenian Opalinuston of Switzerland. This low-oxygen outer shelf environment was dominated by small-sized bivalves, in particular by the pteriod *Bositra*. Analyses of size in low-latitude areas, carbonate settings, and shallow-water habitats each result in a pattern very similar to that of Figure 6A. In the other environmental categories, no consistent trends are evident. Altogether, there is no indication of an increase in the relative occurrences (Fig. 6A) and diversity (Fig. 1C) of large-sized shells in the Jurassic.

Ornamentation

In addition to bivalves, we also analyzed gastropods for trends in ornamentation through time. Contrary to our expectation, however, mean ornamentation of the epifauna remained fairly constant throughout most of the Jurassic (Figs. 1C, 6B) with the lowest values characterizing the two youngest stages (Fig. 6B). In epifaunal bivalves from low latitudes (Fig. 6C), from carbonates, and from shallow-water settings, mean ornamentation became even less prominent after the Early Jurassic, which is opposite to our expectation.

Feeding Mode

Our first-order prediction of a decreasing abundance of suspension feeders due to bioturbation gains little support from our analysis of feeding strategies. On a global scale, the share of suspension feeders varied little over the Jurassic without any long-term trends (Figs. 1B, 7). Only in carbonate environments

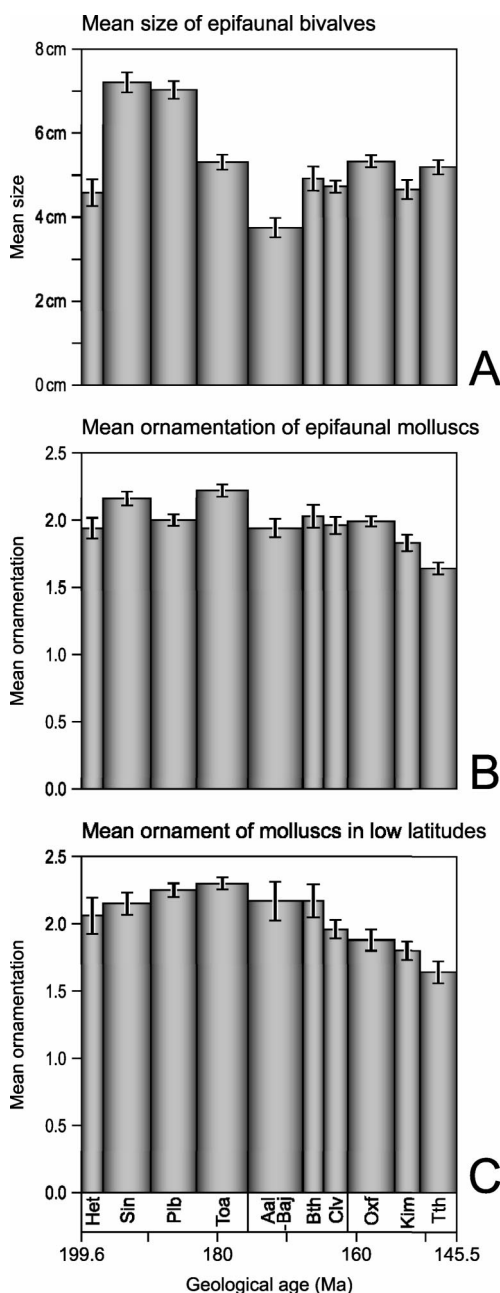


FIGURE 6. Mean size and mean ornamentation of epifaunal species throughout the Jurassic based on taxonomic occurrences. A, Mean size (based on geometric mean of shell length and shell height of largest known specimen of each species) of epifaunal bivalves. Total number of species = 751. B, Mean ornamentation of epifaunal bivalves and gastropods. Total number of species = 1435. For quantifying ornamentation see methods section. C, Mean ornamentation of epifaunal bivalves and gastropods from low latitudes. There is no significant trend in A ($r_s = 0.12$, $p = 0.75$) or B ($r_s = 0.53$, $p = 0.12$); mean ornamentation in low latitudes (C) shows a significant decrease ($r_s = 0.68$, $p = 0.03$). Error bars represent 95% confidence intervals. For legend see Figure 1.

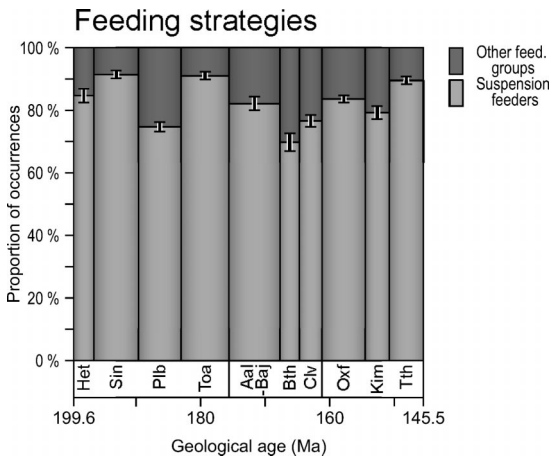


FIGURE 7. Proportion of suspension feeders versus other feeding modes (see Table 2) in Jurassic level-bottom communities based on taxonomic occurrences. No trend is apparent during the Jurassic ($r_s = 0.21$, $p = 0.56$). Error bars for suspension feeders represent 95% confidence intervals. For legend see Figure 1.

is there a moderate and marginally significant decrease in proportional occurrences ($r_s = 0.62$, $p = 0.054$) and diversity of suspension feeders. This can be traced back to a general decline of suspension-feeding brachiopods and the rise of microcarnivorous scleractinian corals.

Discussion

Biotic Interactions as Driving Forces of Evolution

Our analysis yields evidence that increasing predation pressure and bioturbation intensities are paralleled by directional quantitative changes in the composition of the global shelly macrobenthos of the shelf ecosystem. This suggests a causal link between these patterns and implies that biotic interactions were major determinants of the observed macroevolutionary trends.

With respect to the six predation-related predictions outlined above (Table 3), three are strongly supported by the data: an increasing overall mobility, reduction of forms with a free-living mode of life, and increasing colonization of the infaunal habitat. This infaunalization is largely due to the proliferation of shallow infaunal burrowers. The modest contribution of deeply burrowing organisms to this pattern is unlikely to be related to pre-

dation, however, because a proportional increase of this ecological group is concentrated in mid to high paleolatitudes and deeper-water shelf environments, i.e., habitats in which predation (and bioturbation) is considered to be much less severe than in the shallow-water Tropics. It should be noted that the rise of infauna is *relative* to the abundance of epifauna. The epifauna itself may have expanded, but less strongly than the infauna.

The other three expectations (an increasing proportion of cemented as opposed to byssate bivalves, an increasing proportion of large-sized bivalves, and an increasing proportion of strongly ornamented benthic molluscs) were not supported by our analysis. On a global scale, these three features do not show any trend and thus neither support nor contradict our interpretation. It should be noted that trends in maximum size or ornamentation may well have been present within individual evolutionary lineages and thus may yield evidence of escalation at a local scale, but apparently there were no net changes within the entire macrobenthos at a global scale, which is the scope of our study. In this respect, our analyses are different but complementary to the “bottom-up” approach advocated by Vermeij (2002) wherein case studies of the escalation hypothesis are performed within lower-level taxonomic groups in which species share similar phylogenetic backgrounds.

Regarding the analysis of size patterns, our result is somewhat surprising, given the widely recognized evidence of phyletic size increase in Jurassic bivalves (e.g., Hallam 1975, 1998). However, as Hallam (1975) pointed out, a gradual size increase within lineages may have been compensated for by the frequent (and more rapid) evolution of smaller species from larger ones, resulting in no net increase of size during the Jurassic. Large-bodied organisms may have a selective advantage when confronted with predators, but there may be disadvantages as well. Provided that food supply remains approximately constant, larger organisms may face higher extinction risks because of smaller population sizes and longer generation times. Jablonski (1997), in his analysis of body-size changes in Cretaceous bivalves and gastropods, demonstrated that

directional decreases in sizes were as frequent as directional increases and that multiple pressures operate on body size. If coevolutionary alternation (Thompson 2005) was a common phenomenon in the Jurassic, the tendency of attaining large adult size in a species while under continuous attack by a predator may have been reversed during times when a predator focused its attack on other less defended species, or when natural selection favored those predators that preferentially attack the prey species that are currently least protected. Finally, it can be argued that body size, especially of suspension feeders, reflects productivity rather than strict defense against predators, an argument that is in some agreement with the patterns in our data. Maximum size was largest in the Early Jurassic and a large proportion of our data for this time period are from western South America (Table 1). This area had a high probability of conditions favorable for coastal upwelling and therefore high productivity (see paleoclimatic modeling maps of Golonka et al. 1994), but it is under-represented in younger time intervals when data are dominantly from less productive areas in Europe.

The only pattern that is truly at variance with expectations from increasing predation pressure concerns ornamentation. Strong external sculpture is one out of several morphological traits for resisting shell breakage. Besides an increase in size, other antipredatory skeletal features in bivalves include crenulation of the shell margins, high convexity of the valves, increase in valve thickness, and a tight closure of the valves (Vermeij 1987). In gastropods, such antipredatory features include a high-spined shell to allow deep withdrawal of the body, a narrowly elongated aperture, presence of teeth in the aperture, and a thick outer lip (Vermeij 1987). Thus, the absence of an expected trend in a single feature that increases resistance to shell breakage should not be overinterpreted (see also the above comment on the “bottom-up” versus “top-down” approach). Nevertheless, it is interesting to note the difference in response intensity between morphological and behavioral attributes, although the two are not completely independent. The latter are expressed by the capability

of regular locomotion such as crawling, burrowing, or intermittent swimming, and by the way organisms attain stability on the seafloor, particularly with respect to a free-living life habit. In these cases we detected clear temporal trends. In contrast, the overall proportional representation of attributes related to shell form, such as shell size and ornamentation, remained more or less unchanged or was even opposite to the prediction.

By comparison with the predation-based scenario, of the five predictions resulting from the mid-Mesozoic rise of biological bulldozers (Table 3), three of them are strongly supported by our analysis. Similar to the faunal consequences postulated for the predation-based scenario, overall and epifaunal mobility increased, the adoption of a free-living life habit became less common, and infaunal forms became more widespread. The apparent absence of any size-related trends has been discussed above. The lack of a distinct trend in predominant feeding strategies may be partly explained by threshold effects. At low concentrations, benthic organisms may even benefit from the resuspension of fine sediment by deposit feeders and the recycling of food particles into the water column, and the adverse clogging effects occur only at very high concentrations (Thayer 1983 and references therein).

A geographic dissection of trends further corroborates the hypothesis that predation and bioturbation influenced the evolution and distribution of Jurassic macrobenthos. Comparison of data from low paleolatitudes with those from mid and high paleolatitudes reveals that the two most distinct features, increasing mobility and infaunalization, were more pronounced in the paleotropics, i.e., the region where predation pressure and biological reworking are thought to have been highest.

Considering the biotic traits investigated in this study, we are not in a position to perform a ranking of the importance of the two selective agents. Under both scenarios, predation and bioturbation, we expect faunal responses to operate in the same direction, and those that are limited to only one process are not very distinct. This is further complicated by

the fact that many predators are important bioturbators (e.g., many crustaceans, starfish, rays), and within the scope of our analysis it is impossible to separate the biological consequences of their disturbance of the sediment and their predation activities (Thayer 1983). Also, a clear cause-and-effect relationship between infaunalization (which may be due to predation or bioturbation or both and leads to bioturbation) and bioturbation (which in turn may trigger infaunalization) cannot be established.

The multitude of adaptive types, including chemical defenses against enemies (Pawlik 1993), prevents us from confidently assessing trends in the overall escalatory condition of Jurassic macroinvertebrates. Nevertheless, our results provide evidence that escalation has occurred. The concept of escalation regards the enemies of an organism as the major agent of natural selection to which organisms are able to respond evolutionarily (Vermeij 1987; Dietl and Kelley 2002). In contrast to coevolution, where two or more taxa respond to each other (Futuyma and Slatkin 1983), in escalation enemies do not primarily respond to their prey but more likely respond to their own enemies. In the context of our study, both predators and bioturbators can be conceived of as enemies. Whereas predators act directly on prey, the effects of bioturbators are more indirect via disturbance of substrate. In predator-prey systems the relative role of coevolution and escalation is still poorly understood and needs to involve all the species that may influence a particular interaction in a local ecosystem (Dietl and Kelley 2002), something we cannot address with our data. Nevertheless, Dietl and Kelley (2002: p. 353) concluded that "on the scale of evolutionary time, predators of large effect likely control the overall directionality of evolution due to the inequalities of predator and prey in control of resources." In the case of bioturbation, coevolution does not seem to play a role. No mechanism is known to us that would force mobile infaunal organisms to evolve to higher efficiency because ecological groups that are immune to bioturbation become relatively more abundant. Instead, the adoption of a mobile infaunal life habit (with the inevitably associ-

ated bioturbation) is a highly effective adaptive response to increasing stress imposed by enemies such as predators and bioturbators. In summary, the large-scale fossil evidence that can be drawn from the quantitative analysis of Jurassic shelly macrobenthos supports escalation as a highly plausible evolutionary process responsible for the observed trends. The existence of corresponding trends in enemies and their prey, however, does not necessarily exclude alternative scenarios.

Alternative Explanations

Preservation.—We are confident that the observed paleoecological patterns reflect a strong biological signal rather than being artifacts of uneven preservation because (1) throughout the analyzed time interval the same groups of shelly organisms were present; (2) the analysis is limited to fully marine shelf environments; (3) the trends are also evident within single taxonomic groups for which variation in preservability should be limited; (4) preservation of Jurassic benthic invertebrates is not biased by lagerstätten effects, as is the case for Jurassic vertebrates (due to the exceptional preservation, for example, in the Early Jurassic Posidonienschiefer of Holzmaden or the Late Jurassic Plattenkalk of Solnhofen); and (5) there is no reason to assume that the preservability of whole ecological groups, which are polyphyletic in composition, changed systematically to cause gradual changes in ecological abundance. However, apart from, or in addition to, escalation as an extrinsic, biotic forcing mechanism, both intrinsic biological and extrinsic abiotic processes may account for the observed patterns.

Intrinsic Biological Control.—The possibility of an intrinsic biological control of the observed patterns is discussed in the context of the infaunalization trend. Because bivalves represent almost 90% of all infaunal occurrences, the discussion is focused on this group. Burrowing bivalves experienced a spectacular post-Paleozoic radiation (Stanley 1968). It may be that the Jurassic diversification of this group, and its increase in relative abundances as documented herein, was largely due to the acquisition of key adaptive in-

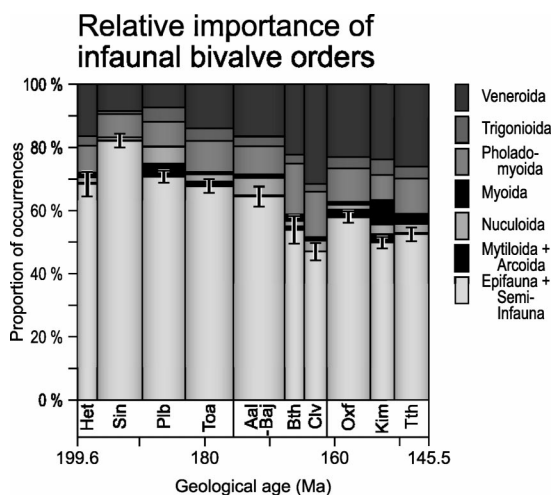


FIGURE 8. Proportion of taxonomic occurrences in Jurassic level-bottom communities within major bivalve orders. Occurrences of epifaunal and semi-infaunal bivalves are combined into one category including epifaunal and semi-infaunal members of the Mytiloidea and Arcoida. Occurrences of infaunal Mytiloidea and Arcoida are shown separately. The Veneroida ($r_s = -0.79$, $p = 0.006$) and Pholadomyoidea ($r_s = -0.67$, $p = 0.03$) show a distinct proportional increase during the Jurassic, whereas such a trend is not evident in the Trigonioidea ($r_s = -0.47$, $p = 0.17$) and Myoidea ($r_s = -0.48$, $p = 0.23$). Error bars for epifaunal and semi-infaunal occurrences represent 95% confidence intervals. For legend see Figure 1.

novations, such as mantle fusion and siphon formation, in only a single or a few clades. If this were the case, the observed infaunalization could be explained by intrinsic biological mechanisms, which were largely independent of the ecological environment. Alternatively, the proliferation of burrowing bivalves may have been more generalized, involving a variety of clades (see also Skelton et al. 1990). Such a pattern would favor a more general cause, such as enemy-induced selection. To distinguish between these two alternatives, we subdivided the infaunal bivalve data into orders and families and contrasted those with epifaunal and semi-infaunal occurrences (Fig. 8). The heterodont Veneroida show the greatest rise in abundance. Within this order, the diverse families Arctiidae and Cardiidae, both siphonate suspension feeders with eulamellibranch gills, contributed significantly to this trend. The Astartidae, which are non-siphonate burrowers with eulamellibranch gills, increased in abundance from Toarcian times

onward. Similarly, the largely edentulous Pholadomyoidea were more common after the Early Jurassic, and the Late Jurassic abundance maxima of the Myoidea can be traced back to the Corbulidae. Both orders have well-developed siphons and eulamellibranch gills. The schizodont Trigonioidea, Recent forms of which are non-siphonate and filibranchiate, play a minor role in the first two stages of the Jurassic but are well represented thereafter. Altogether, the polyphyletic origin of siphons in bivalves (Miller 1990; Skelton et al. 1990) and the independent expansion of burrowers in groups differing in gill type, degree of mantle fusion, and type of dentition strongly argue against a purely intrinsic cause. Moreover, the pattern of increasing numbers of Jurassic infaunal organisms holds true even if bivalves are excluded from the analysis. In a similar way, the overall increase in mobility is not restricted to a single clade but is evident in bivalves, gastropods, and echinoids. Key innovations were certainly necessary to enable organisms to respond to ecological changes, but by themselves they could not have generated phenomena such as the Mesozoic Marine Revolution (see also Vermeij 1995).

Extrinsic Abiotic Control.—It has been suggested that changes in the abiotic environment may produce episodes of escalation. Vermeij (1995) proposed that massive submarine volcanism and the associated effects of climatic warming, sea-level rise, and higher productivity contributed to the early Paleozoic and the latest Triassic to mid-Cretaceous biosphere-scale revolutions. When nutrients and energy are supplied at higher rates, opportunities for innovation and diversification are enhanced. For example, such conditions would permit organisms to adopt energy-intensive modes of life that require high metabolic rates, such as high mobility, and would favor enemy-related adaptations such as the secretion of heavily calcified skeletons. In this scenario, "extrinsic circumstances . . . trigger a cascade of consequences that are controlled by ecological and evolutionary processes intrinsic to organisms" (Vermeij 1995: p. 146). Here, we explore whether abiotic changes alone can be directly responsible for the observed trends.

Fluctuations in environmental parameters

such as water energy, substrate conditions or salinity, and associated biotic changes regularly occur at the local level and over relatively short periods of time. Because most environmental transitions appear to be random or cyclic with respect to time, it is unlikely that the sum of local fluctuations generated the global trends discussed here. Rather, abiotic changes would have to be long term (lasting at least throughout the more than 50 Myr of the Jurassic) and directional. Possible candidates include higher order changes in habitat area, climate, shallow-water productivity, and seawater chemistry.

Jurassic sea-level curves (Hallam 2001) indicate a more or less gradual rise during the period. In combination with the breakup of Pangaea, this led to an enlargement of shelf areas. Although larger shelf areas might possibly favor the relative expansion of groups with traits such as infaunal life habits or high mobility, we failed to find any significant cross-correlations between changes in these ecological traits and changes in sea level.

Climatic warming, combined with high productivity, enables organisms to sustain high metabolic rates, which in turn may foster active behavior such as burrowing, crawling, or swimming. Broad-scale interpretations of Jurassic climates are based upon various lines of paleobotanical, selected lithological, and oxygen isotope evidence, as well as climate modeling studies (Rees et al. 2000 and references therein). Jurassic climate changes have been described for Eurasia (e.g., Vakhrameev 1991) and North America, but Rees et al. (2000) attributed them to the latitudinal motion of continents through climatic zones rather than to a global climate change. On the basis of phytogeographic patterns, these authors recognized five main Jurassic climate zones, the boundaries of which remained at near-constant paleolatitudes. This led them to conclude that net global climate change throughout the Jurassic appears to have been minimal. This view is supported by the distribution of climate-sensitive sediments. Although evaporites became increasingly widespread in the Jurassic, this does not necessarily indicate an increase in aridity. According to Ziegler et al. (2003), this pattern may rather reflect an in-

crease in shallow-water areas due to the spread of epicontinental seas and the opening of the central Atlantic and the west Indian Oceans. Finally, if interpreted in terms of paleotemperature change, the oxygen isotope plot for the Jurassic of Eurasia indicates relatively high temperatures in Hettangian and Early Toarcian time and lowest temperatures in Middle to Late Jurassic time (Veizer et al. 1999; Jenkyns et al. 2002). If water temperature exerted a strong control on the abundance of physically active organisms, we would expect just the opposite pattern, i.e., a decrease in proportional mobility rather than the observed increase. Also, we find no significant cross-correlations between changing proportions of mobile taxa and changes in $\delta^{18}\text{O}$.

Evidence of increasing Phanerozoic nutrient levels and food availability comes from the secular record of strontium isotopes, rates of organic carbon burial, the diversification of marine phytoplankton, and changes in the "energetics" (the combination of biomass, general physical activity, and metabolic rates; Bambach 1999) of the marine benthos (Martin 2003). To avoid circular reasoning we cannot use the observed proportional increase of energy-intensive modes of life to infer greater energy availability. Increased $^{87}\text{Sr}/^{86}\text{Sr}$ ratios generally indicate erosion of continental rocks and have been used as an indicator of increased nutrient runoff from continents (e.g., Martin 2003). The high-resolution strontium isotope curve for the Jurassic (Veizer et al. 1999; Jenkyns et al. 2002) shows relatively high values in the earliest Jurassic, intermediate values from Toarcian to mid-Bajocian time, and lower values thereafter until early Tithonian time. Again, there are no significant cross-correlations between changes in proportions of ecological groups and changes in $^{87}/^{86}\text{Sr}$. Interpretation is hampered, however, because the strontium isotope ratio is also influenced by other factors, particularly the hydrothermal input from mid-ocean ridges. As far as the Jurassic is concerned, changing rates of seafloor spreading and accompanying hydrothermal activity are thought to be the most important controlling factor (Jones et al. 1994). If true, this renders the Jurassic strontium isotope record an unreliable indicator of nutrient

input from land. Similarly, changes in the composition of carbon isotopes in carbonates may reflect the influence of various factors, primarily global changes in the amount of living biomass, in the amount of carbon buried in sediments, and in the degree of oxidation of organic matter (Jenkyns et al. 2002). Finally, Bambach (1999) suggested that the late Mesozoic intensification of biotic interactions was achieved by a biologically controlled increase in nutrient supply to the ocean, caused by the diversification of angiosperms on land. This increase in terrestrial productivity began in the Cretaceous and continued into the Cenozoic and thus postdates the Jurassic changes discussed here.

With respect to seawater chemistry, the Mg/Ca ratio shows secular variations during the Phanerozoic (Stanley and Hardie 1998; Dickson 2002). The Jurassic is characterized by a marked decrease in this ratio (Hardie 1996). This correlates with a shift in the Middle Jurassic from an "aragonite" sea (Sandberg 1983), in which the mineralogy of marine cements and oolites was of aragonite and high-Mg calcite, to a stable "calcite" sea, during which low-Mg calcite dominated mineralogy. It can be argued that aragonite was difficult to maintain at the outer surfaces of shells during highly corrosive calcite seas or even that it may have been difficult to manufacture (Harper et al. 1997). Accordingly, the change from an "aragonite" sea to a "calcite" sea in the Middle Jurassic may have promoted the evolution of less soluble calcitic shells. Thus, the trends reported herein may just be superimposed effects of changes in seawater chemistry. To address this possibility we assigned each taxon in our database to a specific category of skeletal mineralogy: dominantly aragonite or high Mg-calcite; dominantly low Mg-calcite; or mixed aragonite/calcite. Contrary to what we would expect from chemical changes in seawater, we observe a significant increase in the relative abundance of aragonitic/high Mg-calcitic shells (Figs. 1A, 9). If we exclude all organisms that live under the chemically highly variable conditions within the sediment and restrict the analysis to the epifauna, this trend is equally distinct. Even if we take the proportional importance of "sim-

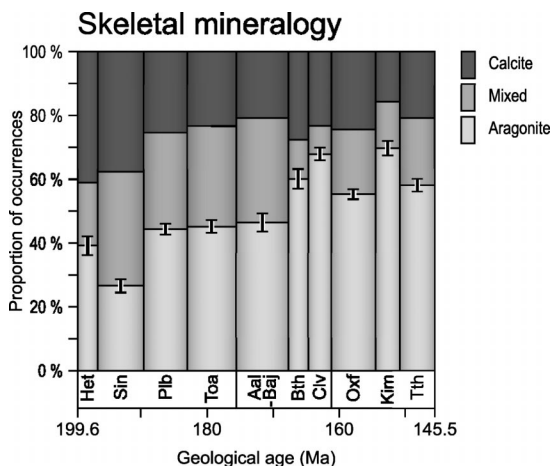


FIGURE 9. Proportion of skeletal mineralogies in Jurassic level-bottom communities based on taxonomic occurrences. Aragonitic taxa exhibit a significant proportional increase during the Jurassic ($r_s = -0.84$, $p = 0.002$). Error bars for aragonitic taxa represent 95% confidence intervals. For legend see Figure 1.

ple" epifaunal taxa that have relatively weak control over the microenvironment in which they secrete their skeleton (corals and sponges), the trend remains. Furthermore, the cross-correlation between changes in the Mg/Ca ratio of seawater and changes in skeletal mineralogy is not significant. In conclusion, the effects of changing seawater chemistry are not reflected in the expected abundance and diversity patterns of Jurassic benthic invertebrates. Provided that the inferred Mg/Ca ratios of Mesozoic seawater are correct, this suggests either that skeletal productivity was independent of the ambient Mg/Ca ratio or that its effects were strongly masked by other factors.

Long-term Trends in the Marine Realm

The question can be asked whether the mid-Mesozoic trends at the scale of tens of millions of years observed here are part of even longer-term patterns, or whether eventually a state of dynamic equilibrium or a reversal in the proportions of functionally distinct biota occurred. Analyses of long-term trends have usually been carried out for specific clades. In the best-studied group, the bivalves, a long-term decline in relative diversity of (endo-)byssate and free-living genera and families at the expense of siphonate free-bur-

rowing suspension feeders is well established (e.g., Stanley 1968, 1977; Thayer 1983; Miller 1990; Skelton et al. 1990). Within brachiopods, the high percentage of free-living genera in the Paleozoic was sharply reduced in the Mesozoic, during which the more bulldozing-resistant, pedunculate guilds strongly dominated the group (Thayer 1983). Published analyses of the long-term functional diversity of gastropods and echinoderms are not available. Attempts to analyze the diversity and/or abundance history of ecological groups of whole faunas have been limited. With respect to well-skeletonized marine benthic invertebrates other than bivalves and brachiopods, Thayer (1983) recorded a post-Silurian to Recent increase in the percentage of mobile higher taxa (families to orders). Aberhan (1994) studied quantitatively the relative abundance of benthic macroinvertebrate species in Mesozoic paleocommunities and documented infaunalization. In particular, in shallow shelf settings a drastic rise of shallow to moderately deep infaunal suspension feeders took place from Late Jurassic to Early Cretaceous time, and the proportion of this guild remained relatively high in Late Cretaceous time. A PBDB-based test of escalation at the scale of the Phanerozoic, including nektonic macroinvertebrates, demonstrates a general increase in the proportion of carnivorous invertebrates, associated with progressive infaunality and mobility in non-carnivorous invertebrates (Madin et al. 2004). These results suggest that the mid-Mesozoic trends of our study may represent segments of megatrends that extend over hundreds of millions of years and across the globe, and that were possibly driven by escalation.

Using a different data set (Sepkoski's genus database as of May 1996), Bambach et al. (2002) calculated proportional diversity of major functional groups through the Phanerozoic. They found that the relative representation of mobile marine metazoans was significantly higher in the Paleogene and Neogene as compared to the Late Triassic to Late Cretaceous, which in turn shows a higher percentage of mobile genera as compared to the Silurian to Permian. Within these intervals of time, however, proportional global diversity

remained stable, despite evolutionary turnover and changes in total diversity. This contrasts with our finding that the proportions of taxonomic occurrences and species of mobile taxa increased from roughly 20% in the Early Jurassic to about 40% at the end of the period. It is unclear at present whether this discrepancy is due to differences in the databases (genera were used by Bambach et al. whereas we analyzed species-level data; vertebrates and nekton were included by Bambach et al. but not in our analysis) or whether it represents a decoupling of diversity and abundance metrics in the database used by Bambach et al.

Conclusions

The evolutionary importance of the ecological interplay between organisms on large temporal and geographic scales has rarely been tested rigorously. In one of the few attempts to study ecosystem-wide faunal changes in terms of ecological dominance (i.e., the abundance of functional groups), we provide detailed insight into the dynamics associated with the Mesozoic Marine Revolution. Our findings of directional trends, e.g., toward increasing mobility and infaunality, suggest escalation between macrobenthic non-carnivorous invertebrates and their enemies (predators as well as sediment disturbers). Thus, we provide evidence of large-scale enemy-driven evolution during mid-Mesozoic time, well before escalation appears to have continued at an accelerated pace in the Cretaceous. Our search for alternative explanations of the observed biotic changes failed to find any evidence that factors other than enemy-induced selection have played a significant role. Neither intrinsic processes, such as the acquisition of key adaptive traits, nor physico-chemical factors, such as changes in sea level, climate, productivity, and seawater chemistry, can explain these patterns. Future research will have to combine abundance and diversity data of ecological groups at the Phanerozoic scale to evaluate the significance of long-term biosphere-level biotic changes.

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