

Paleoecologic Megatrends in Marine Metazoa

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Abstract

Since their appearance in the Neoproterozoic, marine metazoan ecosystems have increased in ecological diversity, complexity, energy use, motility, predation, infaunality, and biological disturbance. A common theme is an increase in organismal control over internal physiology and the external environment. Often, these changes have been examined in the context of discrete events (e.g., the Cambrian Explosion, Mesozoic Marine Revolution), but they may represent linked, ongoing megatrends. This review examines changes in ecological composition in the context of changes in taxonomic composition, as represented by a more detailed version of Sepkoski's evolutionary fauna analysis. Ecological change occurred during major radiations and extinctions, as well as between them. Due to its ecological selectivity, the Permian-Triassic extinction had particularly significant ecological effects on the biota. Recoveries from mass extinctions may be important episodes of ecological change. Further research could help elucidate the fundamental causes of long-term ecological change, including any role played by the environment.

Ecospace:

the combination of fundamental ecological parameters that determines the habitat preferences and mode of life of an organism

INTRODUCTION

Ecology is the study of interactions among organisms and between organisms and their environment; of particular interest are the biological and environmental factors that control the distribution, abundance, and diversity of organisms. Owing to information loss during fossilization and the inability to perform manipulative experiments, paleoecologists cannot study these factors with the same level of detail as ecologists working on living organisms. Although much detail is lost, the fossil record is irreplaceable in understanding how ecology has changed through time. If one generously assumes that the science of ecology began approximately 200 years ago (e.g., the work of von Humboldt), then the fossil record of animals alone increases one's temporal scale of observation by a factor of approximately 3 million.

The fossil record reveals that the ecological interactions and controls that typify modern ecosystems have changed greatly in strength through time and that the present represents just one of many states that have existed during the history of life on Earth. The fossil record also suggests the mechanisms that were probably responsible for episodes of major ecological change. Here, we review some of these major changes with respect to marine metazoan ecosystems and their relationships to evolutionary radiations and turnovers.

SCOPE OF ANALYSIS

This review concentrates on several interrelated themes relevant to ancient organisms and ecosystems. The first theme covers the life habits of fossil organisms, which include parameters related to where and how organisms live and feed. To describe life habits, Bush et al. (2007) and Bambach et al. (2007) defined a theoretical ecospace in which every organism could be classified into an ecological mode of life by combining three fundamental ecological parameters: tiering [position with respect to the sediment-water interface (Ausich & Bottjer 1982, 2001)], motility level, and feeding strategy (see sidebar, Fundamental Paleoecologic Parameters of Fossil Animals; **Figure 1a–c**). These parameters describe the location of an animal's habitat, its ability to respond to disturbance or attack, and its method of acquiring nutrition. Although these parameters simplify reality, they permit reasonable inferences from the fossil record and comparisons across vast stretches of time. Novack-Gottshall (2007) independently devised a similar but more detailed scheme.

The life habits of extinct organisms can be inferred by interpreting functional morphology (e.g., Stanley 1970, Fortey & Owens 1999), comparing with living relatives or analogs, and analyzing biomechanics (Plotnick & Baumiller 2000). As direct records of animal behavior, trace fossils are an important, independent line of evidence on animal ecology. Drill holes and breakage scars provide evidence of predation intensity (e.g., Baumiller & Gahn 2004, Huntley & Kowalewski 2007), and burrows reveal information on infaunal tiering and the disturbance of soft-sediment substrates (e.g., Droser & Bottjer 1989; see below). We examine changes in life habits at several levels of specificity, including presence/absence (e.g., how many ecological lifestyles were utilized at different times?), diversity (e.g., how did the diversity of predators change through time?), and local abundance (e.g., how abundant were different lifestyles within fossil assemblages of different ages?).

The second theme this review considers is disturbance and its influence on ecosystem structure (see sidebar, Disturbance). Disturbance is one of the primary controls on the composition of ecological communities (Stanley 2008, and references therein); it counteracts competitive exclusion or otherwise restricts community membership to organisms that can tolerate the disturbance or quickly colonize afterward. Disturbance is caused by physical agents (e.g., waves, storms), which have presumably remained relatively constant through time, and by the activities of organisms.

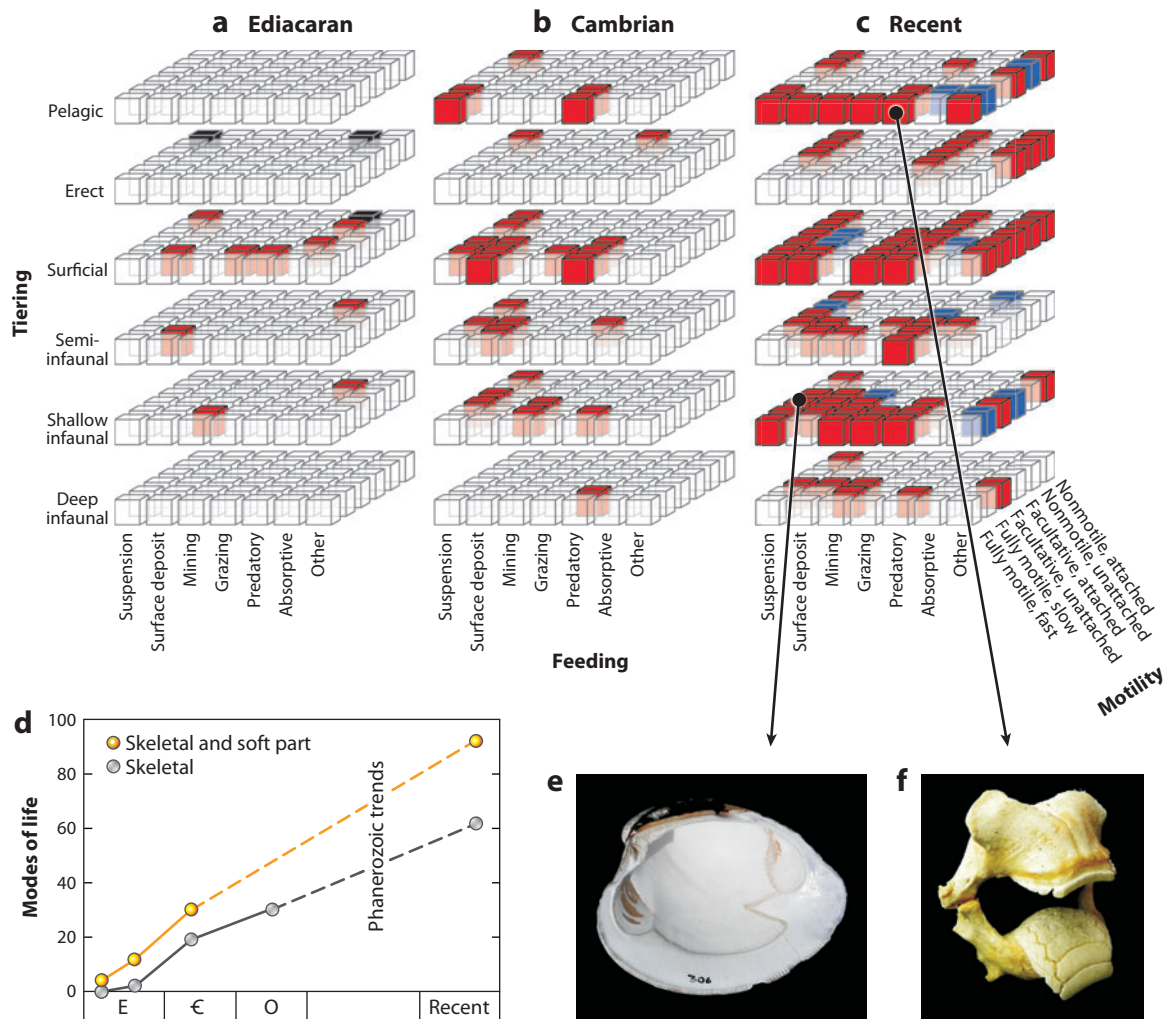


Figure 1

Change in ecospace use of marine metazoa based on the theoretical ecospace of Bush et al. (2007). Each box in panels *a–c* represents a unique combination of ecological characteristics (tiering with respect to the sediment–water interface, motility level, and feeding mechanism). (*a*) Ediacaran Period. Black boxes mark lifestyles that are inferred for animals in both early and later assemblages; red boxes are inferred only for later assemblages. (*b*) Early–Middle Cambrian. Red boxes include both skeletal and soft-bodied assemblages. (*c*) Recent marine metazoa. Red boxes indicate lifestyles inferred for animals that have a diverse fossil record; blue boxes indicate animals that do not. (*d*) Change in the number of modes of life through time based on these data. Panels *a–d* adapted from Bambach et al. (2007), with permission from the Palaeontological Association. (*e*) *Mercenaria mercenaria*, a shallow-infaunal, unattached, facultatively motile suspension feeder. Recent, Cape Cod, USA. (*f*) The jaws of the bat ray *Myliobatis longirostris*, a pelagic, fully motile, fast predator. Its flat tooth plates are used to crush shellfish. Santa Rosalia, Baja California, Mexico. Specimen provided by Janine Caira. Timescale abbreviations: E, Ediacaran; C, Cambrian; and O, Ordovician.

The ability to disturb other animals is thus an important ecological characteristic to track through time.

Finally, we make note of potential changes through time in the amount of energy used by animals (e.g., Vermeij 1987, 1995; Bambach 1993, 1999; Martin 1996, 2003; see sidebar, Energy Use). The amount of primary productivity needed to support an animal depends on factors such as

FUNDAMENTAL PALEOECOLOGIC PARAMETERS OF FOSSIL ANIMALS

The ecological role played by an organism as part of an ecosystem can be characterized by chemical exchanges (e.g., nutrient acquisition, excretion of wastes, respiration), physical modifications to the environment, and interactions with other organisms (e.g., competition, symbiosis). In the fossil record, it is often difficult or impossible to examine many of these processes directly and with the same detail that is available from observations of modern, functioning ecosystems. However, the conditions under which basic ecological interactions occurred and the general strategies for executing basic biological functions can be assessed from the fossil record; for example, one can determine where an animal lived, how it coped with physical stresses intrinsic to that habitat, and the mechanisms it used for acquiring nutrition. These parameters encompass many important life activities and can be compared across hundreds of millions of years. Understanding an organism with reference to these variables permits understanding how it lived and the general challenges to which it was adapted. We discuss three parameters of fundamental interest: tiering, motility, and feeding mechanism. Other parameters can be examined as well, data permitting (e.g., Novack-Gottshall 2007).

Tiering refers to the location in which a marine organism lives with reference to the sediment-water interface (Ausich & Bottjer 1982, 2001). In the oceans, three general habitats impose fundamentally different requirements on animals as they live, feed, and reproduce: in the water mass, on the surface of the seafloor, and within the seafloor or other substrate. Our general tiering spectrum breaks these three habitats into six categories based on the adult animal's position during life:

- 1) Pelagic: in the water column
- 2) Erect: on the seafloor, reaching into the water column
- 3) Surficial: on the seafloor
- 4) Semi-infaunal: partially buried in the substratum
- 5) Shallow infaunal: fully buried, typically in the top ~5 cm of sediment, where coping with disturbance is generally a greater challenge than is maintaining contact with the water column
- 6) Deep infaunal: fully buried, typically deeper than 5 cm, where maintaining contact with the water column requires greater effort

Motility is the ability of an animal to move under its own power. It is considered a fundamental ecological attribute because it determines an animal's ability to acquire resources and respond to threats and disturbances. Motility ranges from fully motile (moving regularly as part of the feeding/living routine) to facultatively motile (moving only in response to threat or disturbance) to nonmotile (no ability for intentional, controlled movement):

- 1) Fully motile, fast: regularly moving, often with limbs, fins, or the like
- 2) Fully motile, slow: regularly moving, but with a strong bond to the substrate (e.g., creeping, gliding)
- 3) Facultatively motile, unattached
- 4) Facultatively motile, attached
- 5) Nonmotile, unattached
- 6) Nonmotile, attached

Attachment to a substrate is here considered as part of motility because attachment is one method of resisting physical disturbance and maintaining position and orientation.

Feeding mechanism is the method by which an animal acquires energy and nutrients, which are fundamental ecological needs by any definition. A fossil organism's specific diet can be difficult to establish, but feeding mechanism

generally can be inferred on the basis of preserved morphology or inferred by phylogenetic comparisons. Animals that utilize different feeding mechanisms play different roles in an ecosystem and face different types of selective pressures. The following are types of feeding mechanisms:

- 1) Suspension feeding: capturing suspended particles from the water column
- 2) Surface deposit feeding: eating detritus from a substrate
- 3) Mining: recovering buried food
- 4) Grazing: rasping or nibbling
- 5) Predation: capturing prey capable of defense or resistance
- 6) Absorptive/Osmotrophic feeding: absorbing nutrients across the body wall
- 7) Other: e.g., chemosymbiosis, photosymbiosis, parasitism; this category can be divided up as needed

Some feeding mechanisms imply a particular diet (e.g., predation implies carnivory), but others can encompass several types of food. If diet is known, then taxa can be classified further using this information.

It is not possible to determine the ecological properties of fossil organisms with the same detail accorded modern organisms; therefore, the ecological categories outlined above have been kept relatively general so that the majority of fossils can be assigned with some degree of confidence. These assignments can be made by analysis of the functional morphology of a fossil (especially with attention to biomechanics; Plotnick & Baumiller 2000) and by analogy with living relatives (especially in cases in which the ecologic property can be considered a synapomorphy for the higher taxon to which the fossil belongs). Stanley's (1970) analysis of bivalves and Fortey & Owens' (1999) analysis of trilobites are excellent examples. Tiering is generally interpretable from fossil material because the physical conditions associated with a tier determine many of the morphological features necessary for success in that setting. Aspects of motility, such as the abilities to move and attach, are often interpretable from analyses of the functional morphology of fossil material because those activities require physical structures that often are preserved or can be interpreted from the preserved fossil and its inferred anatomy. Likewise, the mechanism by which food is acquired is a physical process that often leaves its mark on the morphology of an animal, as do aspects of motility. In cases in which transport after death was minimal, the sedimentology of the bed in which a fossil was preserved may provide useful data on habitat.

These concepts are discussed in detail by Bush et al. (2007) and Bambach et al. (2007). The modes of life specified by our scheme are illustrated in **Figure 1a–c**.

its metabolic rate, biomass, temperature, and trophic level (Payne & Finnegan 2006). The biomass of an extinct organism can only be estimated, of course, but in general this can be done reliably for comparisons among taxa (e.g., Kosnik et al. 2006, Novack-Gottshall 2008b). Our understanding of changes in energy use through time is preliminary, but some intriguing studies have come out recently.

We lack the room to discuss the potential relationships of many abiotic factors to the patterns documented here, but all organisms have many physiological requirements that can affect patterns of extinction, radiation, and distribution (e.g., Stanley 2006, Knoll et al. 2007a, Pruss et al. 2010). More information on the influence of abiotic factors on the ecological record of the history of life will emerge as the field of geobiology advances.

PHANEROZOIC DIVERSITY: TWELVE FAUNAS

Changes in taxonomic composition provide useful context for understanding changes in ecology because certain higher taxa/clades are characterized by certain ecological properties and because major changes in taxonomic and ecologic composition coincide to some extent. Sepkoski's (1981)

DISTURBANCE

In this review, the term disturbance refers to the physical movement or reorientation of an organism resulting from the movement of other organisms or from physical events (e.g., storms, currents). Many modern animals are motile and have the potential to act as agents of disturbance. To cause disturbance, an animal may contact other organisms directly or it may disrupt the substrate on or in which they reside. Bioturbators, which burrow in and mix unconsolidated sediments, are particularly potent agents of disturbance. By destabilizing the upper layer of sediment, they can structure entire communities, acting as ecosystem engineers (Berke 2010, Woodin et al. 2010). For example, Clifton (1971) found that 40–60% of shells placed on the sediment surface were buried by sediment mixing in just 40 days without help from storms or strong currents.

Mass extinction: an increase in extinction rates that significantly reduces biodiversity, usually in many different taxa

three-faunas analysis is the classic description of taxonomic turnover in the marine realm; these faunas are statistical groupings of taxonomic classes that have similar diversity histories in geological time. The Cambrian fauna diversified rapidly in the Cambrian but declined rapidly thereafter, whereas the Paleozoic fauna expanded during the Ordovician, was dominant throughout the Paleozoic, and suffered greatly in the end-Permian extinction. The Modern fauna was present at low diversity in the earlier Paleozoic, diversified more slowly than the other two faunas, weathered mass extinctions fairly well, and came to dominate the modern world.

To examine taxonomic turnover at a finer scale, we performed a similar analysis after dividing the largest classes in Sepkoski's database into smaller units (of course, Sepkoski knew that a more detailed analysis was possible; the simplicity of his original analysis was part of its appeal). We used his genus-level database (version provided to Bambach in 1996, similar to Sepkoski 2002) and split the 10 most genus-rich classes into orders, superorders, or subclasses. These classes were the Articulata (Rhynchonelliformea), Gastropoda, Cephalopoda, Trilobita, Bivalvia, Anthozoa, Ostracoda, Osteichthyes, Crinoidea, and Stenolaemata. These diverse, long-ranging classes contained multiple large subtaxa that had variable ecological properties and/or diversity histories. Our units of analysis thus are not taxonomically consistent, but ranks in the Linnaean hierarchy are not necessarily equivalent anyway, and our grouping of taxa permits us to see details of taxonomic turnover not accessible in Sepkoski's (1981) analysis.

Metazoan taxa that contained 30 or more genera were included, although a few less diverse ones from the Cambrian also were included because they constituted a greater proportion of the per-interval total. We were most interested in trends in the relative importance of taxa, so for each time interval, numbers of genera were converted to proportions. The use of proportions also alleviates concerns about biases that may affect trends in total diversity through time (e.g., Alroy et al. 2008). We began the analysis at the Atdabanian because the earliest stages of the Cambrian had a greater proportion of small and/or problematic taxa. We used cluster analysis rather than factor analysis because it assigns taxa completely to a fauna rather than calculating loadings on

ENERGY USE

The term energy use refers to the caloric demands of metabolism. On an equal-biomass basis, actively motile animals (especially predators that also must use energy to subdue their prey) use more energy than do attached animals that obtain food by suspension feeding. Similarly, the energy demands of a community dominated by sessile suspension feeders (the typical local community of the early and mid-Paleozoic) were less than those of a modern benthic community, in which 80% of the individuals are motile. This topic is discussed fully by Bambach (1993, 1999).

multiple factors (see also Adrain et al. 1998). Taxa were clustered using paired-group linkage and Manhattan distance. The average per substage diversity of each taxon was equalized before clustering, which prevented spurious placement of low-diversity taxa.

This analysis requires several caveats. Working at a higher or lower taxonomic level would yield different clusters that would show different levels of detail, so these results are of course just one possible outcome. Sepkoski's data set is becoming out-of-date in numerous respects, although it is still the best available for our purpose. Some stratigraphic intervals and their names have been revised or replaced, and the taxonomy of some groups is in need of revision [e.g., gastropods (Bouchet & Rocroi 2005)]. Despite these concerns, the analysis reveals several interesting patterns regarding the timing of biotic turnovers.

On the basis of the cluster analysis, we placed 102 higher taxa into 12 faunas (**Figure 2a**), and all but one corresponded to well-defined clusters [the exception being fauna 8; the composition of the faunas is listed in **Supplemental Figure 1** (follow the **Supplemental Materials** link from the Annual Reviews home page at <http://www.annualreviews.org>)]. If the Ediacaran-Tommotian were included, there would have been additional clusters as well. Faunas replaced each other rapidly in the early Phanerozoic as higher taxa radiated and went extinct swiftly (**Figure 2b,c**). This corresponds to the previously observed decline in rates of extinction and origination through the Phanerozoic, with volatile taxa going extinct early and extinction-resistant ones persisting (e.g., Raup & Sepkoski 1982, Gilinsky 1994, Stanley 2007, Wang & Bush 2008).

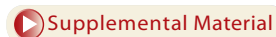
The 12 faunas are grouped into three superclusters that are associated with the Cambrian, Paleozoic, and post-Paleozoic (**Figure 2a**), but they do not correspond directly to Sepkoski's (1981) three faunas because we divided the most diverse classes into subtaxa that had variable diversity histories. Therefore, our 12 faunas are not simple subdivisions of Sepkoski's three faunas. For example, trilobite subtaxa were distributed among faunas 1–4 and 6, which belong to both the Cambrian and Paleozoic superclusters (**Figure 2a**; see also Adrain et al. 1998). At this level of resolution, there is also considerably more turnover among faunas than in Sepkoski's (1981) analysis. Some of this turnover is associated with mass extinctions: not only is the end-Permian extinction apparent, but extinctions in the Ordovician, Devonian, Triassic, and Cretaceous either truncated or permanently reduced the diversity of several faunas. Between mass extinctions, there was slow turnover in relative dominance as one fauna declined in diversity or was diluted by another (e.g., the turnover between faunas 6 and 7–9 in the Paleozoic and faunas 9 and 11 in the Mesozoic). Major increases in biodiversity are associated with the radiation of new higher taxa (i.e., new faunas); this can be seen in **Figure 3a** for the Cambrian (fauna 1), Ordovician (primarily fauna 6), and Mesozoic-Cenozoic (faunas 11–12).

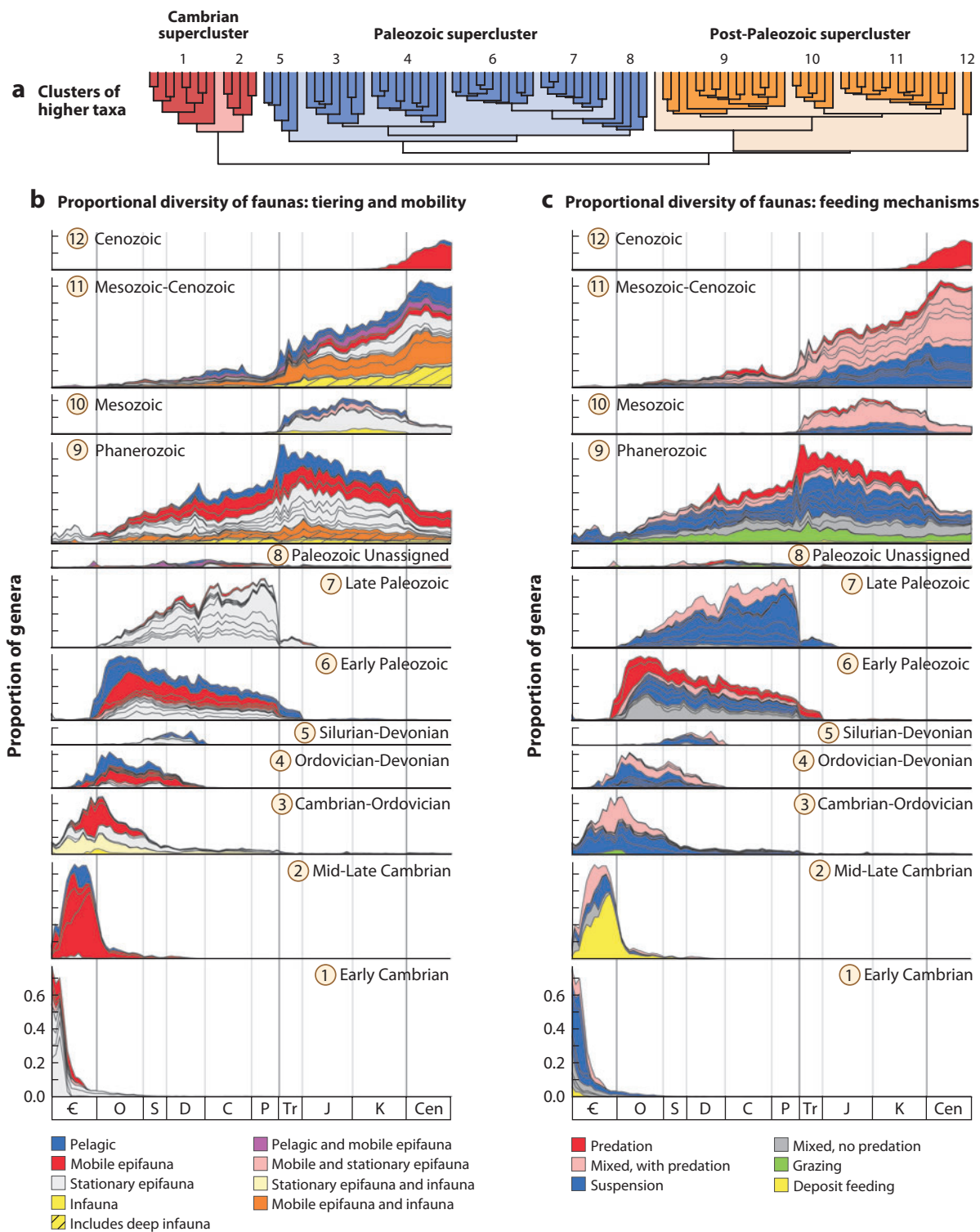
The proportional diversity of the faunas is shown in **Figure 2b,c**, with colors indicating the principal vertical tier and motility level (**Figure 2b**) and feeding mechanism (**Figure 2c**) employed by each higher taxon. Intermediate colors in **Figure 2b** indicate that two ecological categories were represented with some abundance (e.g., a combination of mobile epifauna and infauna; see the **Supplemental Appendix** for ecological assignments). This analysis is intended only to portray first-order trends and patterns; we have not categorized each genus individually.

This analysis is referenced in more detail in the following sections as we discuss major changes in ecology through metazoan history, beginning in the Neoproterozoic. Some ecological changes in the marine realm can be understood in terms of these faunas, whereas other changes are examined with other data.

CHANGES IN ECOLOGY THROUGH TIME

In this section, we discuss major changes in metazoan ecology from the Neoproterozoic to the present, with reference to organismal life habits, disturbance rates, and energy use.





Ediacaran Radiation

Molecular biomarkers of sponges have been found in the Cryogenian (~850–635 Mya; Love et al. 2009), so suspension feeding presumably was present at this time. The first macroscopic fossils generally agreed to be of animals date from the latter part of the Ediacaran Period (Narbonne 2005, Xiao & Laflamme 2009), and the morphology of many forms is consistent with an osmotrophic lifestyle, absorbing nutrients directly from the water column or sediment surface (Laflamme et al. 2009). The earliest assemblages (Avalon-aged) display limited ecological variety (**Figure 1a**; Bambach et al. 2007); mechanisms of food acquisition were apparently limited to osmotrophy and suspension feeding, although erect epifaunal tiers accessed food in the water column (**Figures 1a** and **3b**; Clapham & Narbonne 2002). Apparently, epifaunal tiering was fairly simple to develop compared with other aspects of ecospace occupation. Recently discovered trace fossils suggest that surficial motility may have been present (Liu et al. 2010).

Later Ediacaran assemblages were more diverse ecologically (**Figure 1a,d**). New feeding mechanisms were present; *Kimberella* grazed on microbial mats (Fedonkin et al. 2007), and horizontal burrows suggest deposit feeding. These burrows also indicate that animals had invaded the infauna, however minimally. Several other taxa had at least some motility (e.g., Ivantsov & Malakhovskaya 2002, Dzik 2003, Gehling et al. 2005). The latest Ediacaran assemblages display a few additional ecological innovations. The first biomineralized metazoans appeared (e.g., Grotzinger et al. 2000), and borings in them indicate that predation might have been present (Bengtson & Zhao 1992, Hua et al. 2003). Some large-bodied Ediacarans lived infaunally or semi-infaunally (**Figure 1a**; Grazhdankin & Seilacher 2002).

Rates of biological disturbance on the seafloor were minimal. There is no clear evidence of rapidly motile animals (**Figure 1a**), and predation was limited. Burrowing was so limited and ineffective at stirring the sediment–water interface that microbial mats probably covered much of the seafloor, providing a firm substrate and food for animals (Seilacher & Pflüger 1994, Bottjer et al. 2000).

Cambrian Explosion

During the Cambrian Explosion, most animals with modern morphologies appeared in the fossil record, and with these morphologies came modern ways of interacting with the environment (Zhuravlev & Riding 2001, Marshall 2006, and references therein). Thus, the Cambrian Explosion marks a fundamental turning point in both metazoan evolution and ecology. The osmotrophic Ediacaran animals declined, and suspension feeding became more prominent (e.g., brachiopods, hyolithids, echinoderms). However, osmotrophy continued to be important because sponges feed by absorption as well as from suspension, and they were prominent in the Cambrian [archaeocyaths in the Early Cambrian fauna, other sponges in the Phanerozoic fauna (**Figure 2c**)]. In fact, sponges

Ediacaran Period: geological time period lasting from 635 to 542 Mya, notable for the first animal body fossils; it precedes the Cambrian

Microbial mat: sticky, sheet-like colony of microorganisms that can form at the sediment–water interface, among other places

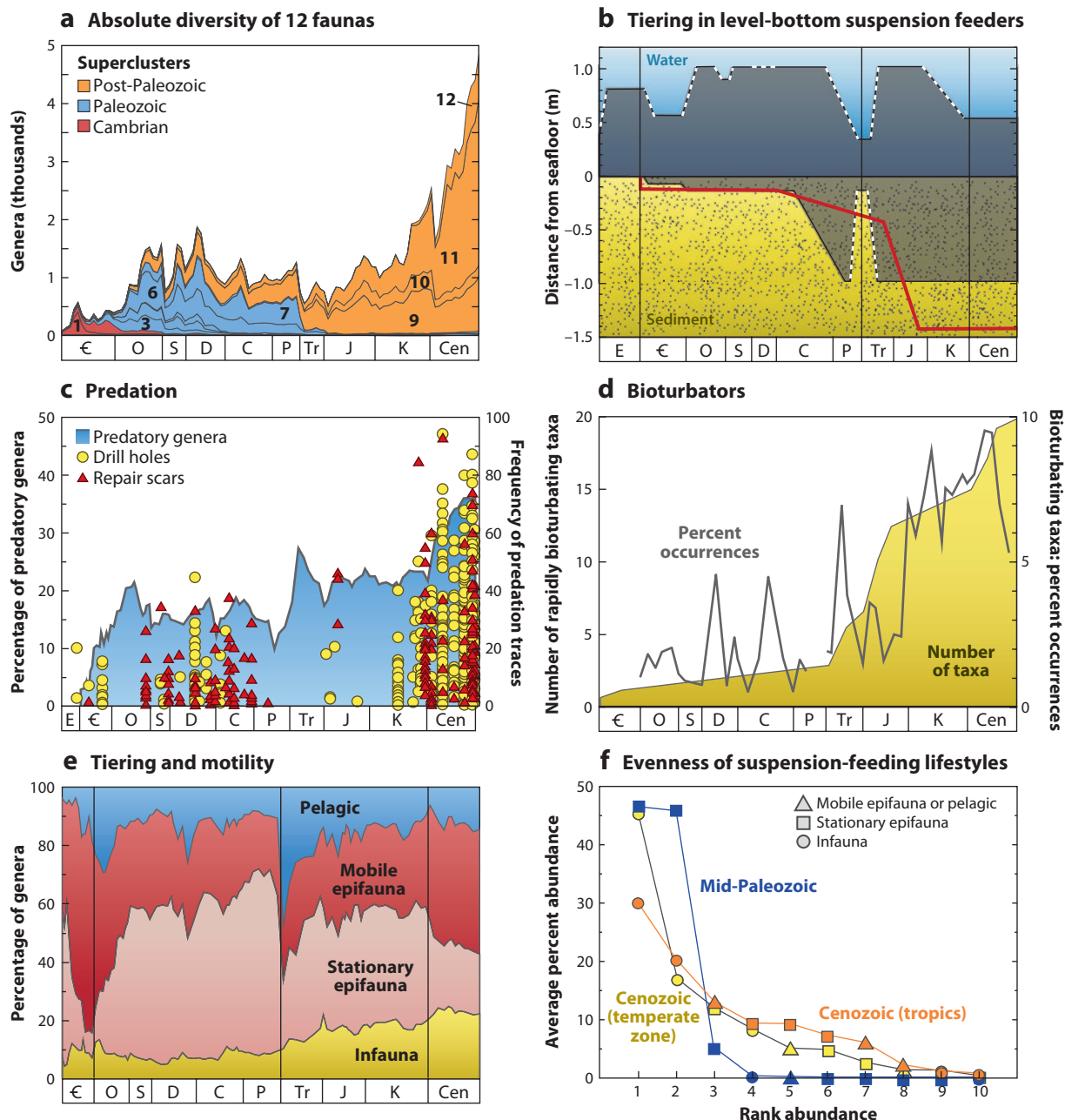
Cambrian Explosion: time of appearance of widespread, mineralized animal fossils, as well as fossils belonging to modern animal phyla

Figure 2

Sepkoski's compendia of genera divided into 12 faunas. (a) Cluster analysis of 102 higher taxa (see **Supplemental Figure 1** for the members of each cluster). (b) Proportional diversity of each cluster through time, beginning with the Atdabanian stage of the Cambrian. Each higher taxon within each cluster is colored according to its dominant tiering/motility level (see the data in the **Supplemental Appendix** for assignments). Mobile epifauna includes fully motile and unattached, facultatively motile lifestyles; stationary epifauna includes nonmotile and attached, facultatively motile lifestyles. (c) As in panel b, but with higher taxa coded by feeding mechanism. Timescale abbreviations: €., Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; and Cen, Cenozoic.

occupied the erect tier on the seafloor during the Cambrian (**Figure 3b**); bilaterian animals did not evolve tall, erect forms until the Ordovician (Ausich & Bottjer 2001, Yuan et al. 2002).

An increase in predation was also a hallmark of the Cambrian (**Figure 3c**; Vermeij 1987, Babcock 2003)—in fact, the advent of predation and other forms of carnivory has been implicated as a trigger of the Cambrian Explosion (e.g., Stanley 1973, Vermeij 1990, Bengtson & Zhao 1992, Bengtson 2002, Marshall 2006). Predators during the Cambrian included a variety of trilobites



(Fortey & Owens 1999, Babcock 2003) and cnidarians, as well as unskeletonized taxa observed in the Burgess Shale and Chengjiang biotas (Briggs et al. 1994, Hou et al. 2004). The advent of numerous consumers such as predators during the Cambrian Explosion marks the lengthening of marine food chains, and the increase in a variety of energy-intensive behaviors [e.g., swimming, burrowing, and crawling (**Figure 1b**)] likewise indicates increasing energy consumption by animals. Other feeding types such as deposit feeders and grazers became abundant for the first time as well (**Figures 1b** and **2c**).

During the Cambrian Explosion, disturbance on the seafloor increased significantly. Ediacaran sediments display little or no bioturbation (the stirring and mixing of sediment by the burrowing activities of animals), but burrows such as the trace fossil *Treptichnus pedum* that have shallow vertical shafts penetrate Lower Cambrian sediments (Droser et al. 2002), and the depth and intensity of burrowing increased from there (**Figures 3b,d** and **4a**; Droser & Bottjer 1989). As a result, microbially stabilized substrates were replaced by the unconsolidated, dynamic sedimentary substrates that characterized most of the rest of the Phanerozoic [the Cambrian Substrate Revolution (Seilacher & Pflüger 1994, Bottjer et al. 2000)]. This change had a profound impact on metazoan communities inhabiting unconsolidated sediments—animals adapted to attachment on microbial mats had to move to different habitats, adapt to less stable substrates, or face extinction. For example, the proportion of echinoderms adapted to microbial mat substrates plummeted (**Figure 4a**; Dornbos 2006).

On the basis of the data shown in **Figure 1**, Bush et al. (2011) concluded that Ediacaran ecosystems, on one hand, were quite unlike Phanerozoic ones with respect to the proportion of modes of life in different tiering, motility, and feeding categories. Cambrian ecosystems, on the other hand, bore some resemblance to modern ones (see also Dunne et al. 2008). However, the number of ecological modes of life has increased since the Cambrian (**Figure 1d**), although the magnitude of the increase may be overestimated somewhat due to preservational biases (Bambach et al. 2007, Hendy et al. 2009).

Numerous ecological parameters, such as the proportion of genera in different motility groups (**Figure 3e**), fluctuated dramatically in the Cambrian due to rapid evolutionary turnover, low total diversity, and the variable ecologic composition of successive faunas (**Figure 2**, faunas 1–3). For example, the sessile, epifaunal archaeocyath sponges were diverse members of the short-lived Early Cambrian fauna, which was replaced by the Mid-Late Cambrian fauna, in which motile trilobites were diverse (**Figure 2b**). The dominance of feeding types also fluctuated dramatically

Burgess Shale and Chengjiang biotas:

exceptionally preserved Cambrian-aged fossil assemblages that contain nonmineralized animals and algae

Figure 3

Phanerozoic-scale changes in paleoecology. (a) Absolute genus diversity of the 12 faunas from **Figure 2**. Faunas are arranged in order; only the more diverse ones are labeled. (b) Tiering. The gray field represents the characteristic maximum height and depth of epifaunal and infauna tiering in shallow subtidal, level-bottom suspension feeders (adapted from Ausich & Bottjer 2001). Dotted lines indicate uncertainty. The red line is the maximum average depth of bioturbation (adapted from Thayer 1983). (c) Predation. The solid line is the proportion of predators in the global marine fauna, based on Sepkoski's genus compendium (adapted from Bambach et al. 2002). The circles and triangles represent the frequency of specimens with drill holes and marginal repair scars, respectively (adapted from Huntley & Kowalewski 2007). (d) Abundance/diversity of bioturbators. The yellow field represents the number of rapidly bioturbating taxa (adapted from Thayer 1983), and the gray line denotes the proportion of occurrences of bioturbating taxa in the Paleobiology Database (adapted from Madin et al. 2006b). (e) Proportional diversity of different tiers and motility levels, based on Sepkoski's genus compendium. The mobile and stationary epifauna are as defined in **Figure 2b**. (f) Average proportional abundances of suspension-feeding modes of life for mid-Paleozoic and late Cenozoic fossil assemblages (data from Bush et al. 2007). Cenozoic assemblages have a more even distribution of modes of life, on average, and most of these modes are infaunal or motile. Timescale abbreviations: E, Ediacaran; C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; and Cen, Cenozoic.

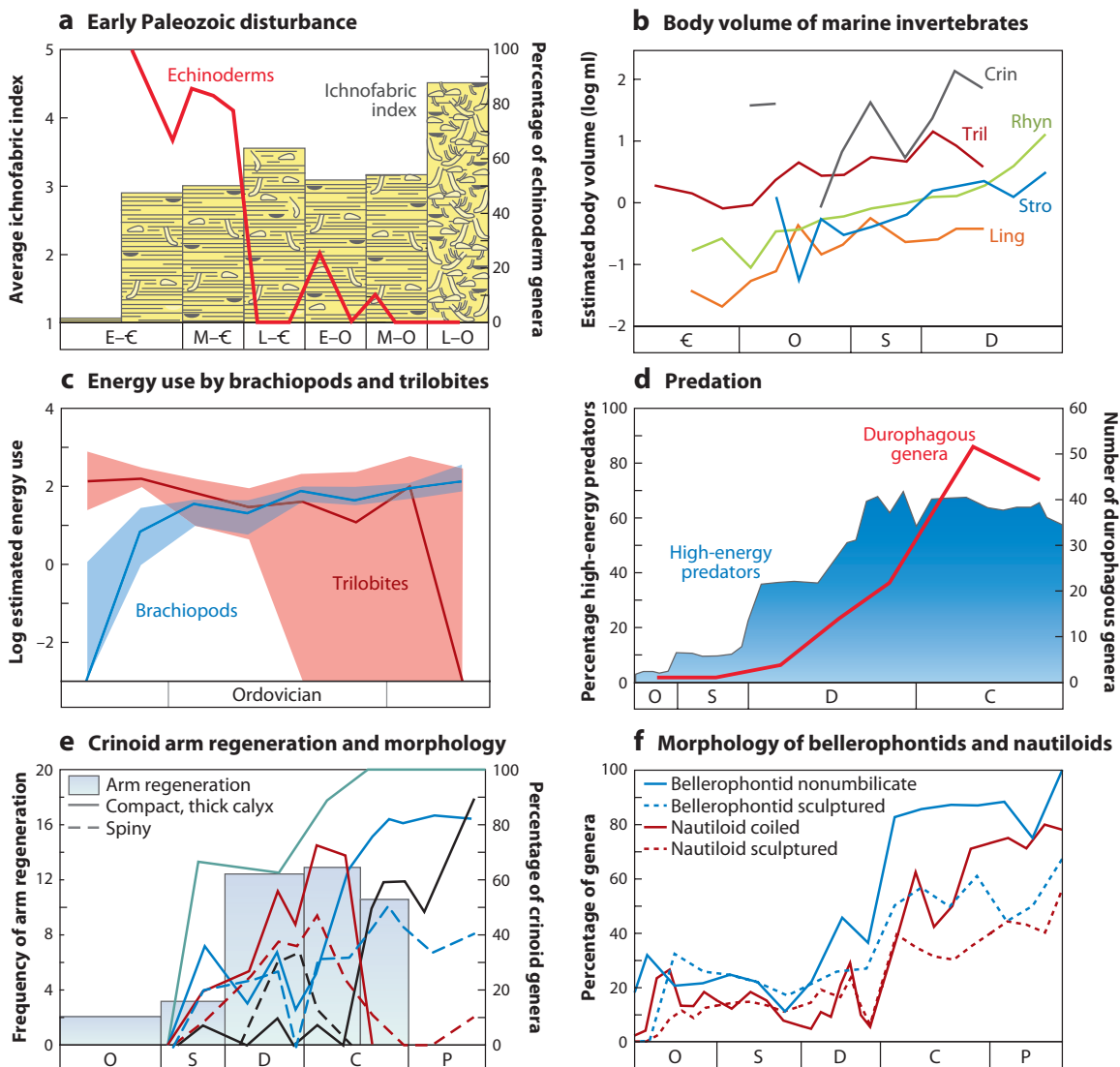


Figure 4

Ecologic changes during the Paleozoic. (a) Increase in average ichnofabric (a measure of burrowing intensity and thus disturbance in soft-sediment habitats) during the Cambrian and Ordovician of the Great Basin, United States (adapted from Droser & Bottjer 1989). As sedimentary substrates became destabilized, the proportion of echinoderms adapted to microbial mat substrates declined (red line; adapted from Dornbos 2006). (b) Trends in average body volume in various invertebrates (adapted from Novack-Gottshall 2008a, with permission from the Paleontological Society). Crin, crinoids; Tril, trilobites; Rhyn, rhynchonellate brachiopods; Stro, strophomenate brachiopods; and Ling, lingulate brachiopods. (c) Change in estimated energy use by brachiopods and trilobites in fossil assemblages from the United States, based on body size and relative abundance (adapted from Finnegan & Droser 2008). Medians and interquartile ranges. (d) Increase in the ratio of high-energy to low-energy predators (blue region; adapted from Bambach 1999) and in the diversity of durophagous predators (red line; adapted from Signor & Brett 1984). (e) Arm-regeneration frequencies in crinoids (bars, with no data for the Permian; adapted from Baumiller & Gahn 2004), a measure of predation intensity. Relative diversity of crinoid genera with various antipredatory morphologies (lines, with colors indicating different higher taxa; adapted from Signor & Brett 1984). (f) Proportion of bellerophonitid and nautiloid genera with various antipredatory morphological characters (adapted from Signor & Brett 1984 and Vermeij 1987). Timescale abbreviations: E, Early; M, Middle; L, Late; Є, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; and P, Permian.

as these faunas replaced each other (**Figure 2c**). During the Ordovician Radiation, total diversity increased, evolutionary turnover slowed, a broader range of ecological lifestyles diversified, and the proportions of different ecological types in the global fauna stabilized. The global ecological instability of the Cambrian was only seen again during the Triassic, when diversity was again extremely low due to the end-Permian extinction (**Figures 2 and 3e**). Many of the ecological changes that have occurred since the Cambrian can be seen as extensions of trends that began at that time, such as increasing biological disturbance, increasing use of available habitat and energy resources, and increasing predation.

Ordovician Radiation

Biodiversity in the oceans increased during the Ordovician Radiation, and new taxa came to dominate (Sepkoski's Paleozoic fauna, faunas 4–9 in **Figures 2 and 3a**). The number of ecological modes of life increased as ecological complexity increased (**Figure 1d**; Bambach 1983, Bambach et al. 2007). Epifaunal tiering increased in height and complexity as bilaterians invaded the high erect tiers (**Figure 3b**). Yuan et al. (2002) suggested that the Cambrian Substrate Revolution might be responsible for this reorganization of epifaunal tiering. Many of the taxa that proliferated in the Ordovician Radiation were epifaunal suspension feeders such as brachiopods, bryozoans, and crinoids; the proportion of stationary epifaunal genera (**Figure 3e**) surged during the Ordovician as these groups diversified (see faunas 3–9 in **Figure 2b**). Infaunal burrowing increased somewhat as well (**Figures 3b and 4a**), leading to declines in sedimentary fabrics such as flat-pebble conglomerates (Sepkoski 1982, Sepkoski et al. 1991).

There was turnover in the water column as well, with graptolites, conodonts, and nautiloids radiating (see faunas 4 and 6 in **Figure 2b**) while the agnostid trilobites declined (fauna 2). Although trilobites are thought of as part of the Cambrian fauna (Sepkoski 1981), several groups radiated later (e.g., proetids, odontopleurids, lichids, phacopids) and are included here among the epifaunal mobile groups in faunas 4 and 6 in **Figure 2b** (see also Adrain et al. 1998). The proportion of predators in the global fauna continued to increase in the Ordovician, then remained relatively stable for the rest of the Paleozoic (**Figures 2c and 3c**; Bambach et al. 2002). These predators included various trilobites (e.g., Fortey & Owens 1999), conodonts, and nautiloids. The microcarnivorous corals also radiated, with the tabulates grouping in the Early Paleozoic fauna and the rugosans in the Late Paleozoic fauna (**Figure 2c**).

The increased diversity, ecospace use, and predation during the Ordovician Radiation probably reflect increased energy consumption by animals. Novack-Gottshall (2008a) found that the average body size of several marine invertebrate taxa (but not mollusks) increased at this time (**Figure 4b**), which he attributed to increased energetics. Likewise, Finnegan & Droser (2008) estimated that energy use by brachiopods increased substantially during the Ordovician Radiation while that by trilobites remained relatively constant (**Figure 4c**). They suggested that brachiopods and other filter-feeding members of Sepkoski's Paleozoic fauna diversified by taking advantage of food resources that were not utilized previously (cf. Westrop & Adrain 1998).

A mass extinction in the Late Ordovician was taxonomically severe but had few long-term ecological effects (Sheehan 2001, McGhee et al. 2004). It affected the Early Paleozoic fauna more than the other faunas, as seen in a loss in proportional diversity (**Figure 2**).

Middle and Late Paleozoic

There was considerable taxonomic turnover between the early and late Paleozoic. The dominant Cambrian groups (faunas 1–3) faded away by the Silurian and Devonian, during which times

faunas 4 and 5 suffered from extinction (**Figure 2**); the Devonian was a time of complex diversity dynamics (e.g., Raup & Sepkoski 1982, McGhee 1996, Copper 2002, House 2002, Bambach et al. 2004, Sallan & Coates 2010). Meanwhile, the Early Paleozoic fauna (fauna 6) declined steadily in relative diversity, and the Late Paleozoic and Phanerozoic faunas (faunas 7 and 9) increased.

The ecological transition from the Early to Late Paleozoic has been termed the Mid-Paleozoic Marine Revolution (Signor & Brett 1984, Brett & Walker 2002, Brett 2003), and it involved increased predation and biotic disturbance. The proportion of predators in the global fauna did not increase (**Figure 3c**), but durophagous (shell-crushing) predators proliferated (**Figure 4d**), particularly among the jawed fish (Signor & Brett 1984). This change also is reflected in an increase in predators inferred to have high metabolic rates (**Figure 4d**; Bambach 1999). Dahl et al. (2010) proposed that rising oxygen levels in the Devonian permitted the diversification of large, predatory fish. The incidence of shells with healed predation scars did not increase (**Figure 3c**; however, see Alexander 1989). The observed frequency of shell drilling did increase in the Devonian (**Figure 3c**), although some Paleozoic drill holes may represent parasitism rather than predation (Baumiller 1990, Baumiller & Gahn 2002). The frequency of arm regeneration rose in crinoids, indicating an increase in cropping predation (**Figure 4e**; Baumiller & Gahn 2004).

At the same time that shell-crushing predators radiated in the Devonian and Carboniferous, shell morphologies that may have protected against crushing increased in many taxa. **Figure 4e,f** shows examples for crinoids, bellerophonitids, and nautiloids. In fact, nautiloids invaded a novel region of morphospace in the Carboniferous, corresponding to smooth, coiled shells that probably represent increased swimming efficiency and predation deterrence (Low 2004). Although immobile crinoids dominated until the Mesozoic, some crinoids in the late Paleozoic may have been motile (**Figure 5a**), which could be related to increased predation or disturbance rates. Productids were the dominant group of strophomenid brachiopod in the late Paleozoic (fauna 7 in **Figure 2**), and they had spines to anchor them in the sediment or to deter predators or both (Signor & Brett 1984; Bambach 1985, 1999; Leighton 2001).

Infaunality increased in the late Paleozoic as well, as seen in the maximum depth of burrowing (**Figure 3b**) and the proportion of infaunal genera in the global biota (**Figure 3e**). In Madin et al.'s (2006b) compilation of the abundance of bioturbators, the first large peaks (up to 10%) occurred in the Devonian and Carboniferous (**Figure 3d**).

Several lines of evidence, such as the increase in high-energy predators, suggested to Bambach (1999) that the energetics of the marine biosphere might have increased from the early to the late Paleozoic. On this note, body size in many marine invertebrates continued to increase during the middle Paleozoic (**Figure 4b**), which Novack-Gottshall (2008a) attributed to increased energetics.

Permian-Triassic

The end-Permian extinction was one of the most important events in metazoan history, eliminating some 69% of marine genera (Bambach et al. 2004). It was strongly selective, as shown by the faunas in **Figure 2b,c**. The Late Paleozoic fauna (fauna 7) radiated throughout the Paleozoic but was nearly eliminated at the end of the Permian; it included such common taxa as rugose corals, productid and spiriferid brachiopods, fenestrate and cystoporate bryozoans, and numerous stalked crinoids. It was dominated heavily by stationary epifaunal suspension feeders, and these forms were decimated in the extinction. In fact, the extinction probably did not select against this ecological lifestyle per se; rather, it preferentially eradicated heavily calcified organisms with little physiological control over mineralization (Knoll et al. 2007a), and these traits were common in the stationary epifauna of the Permian.

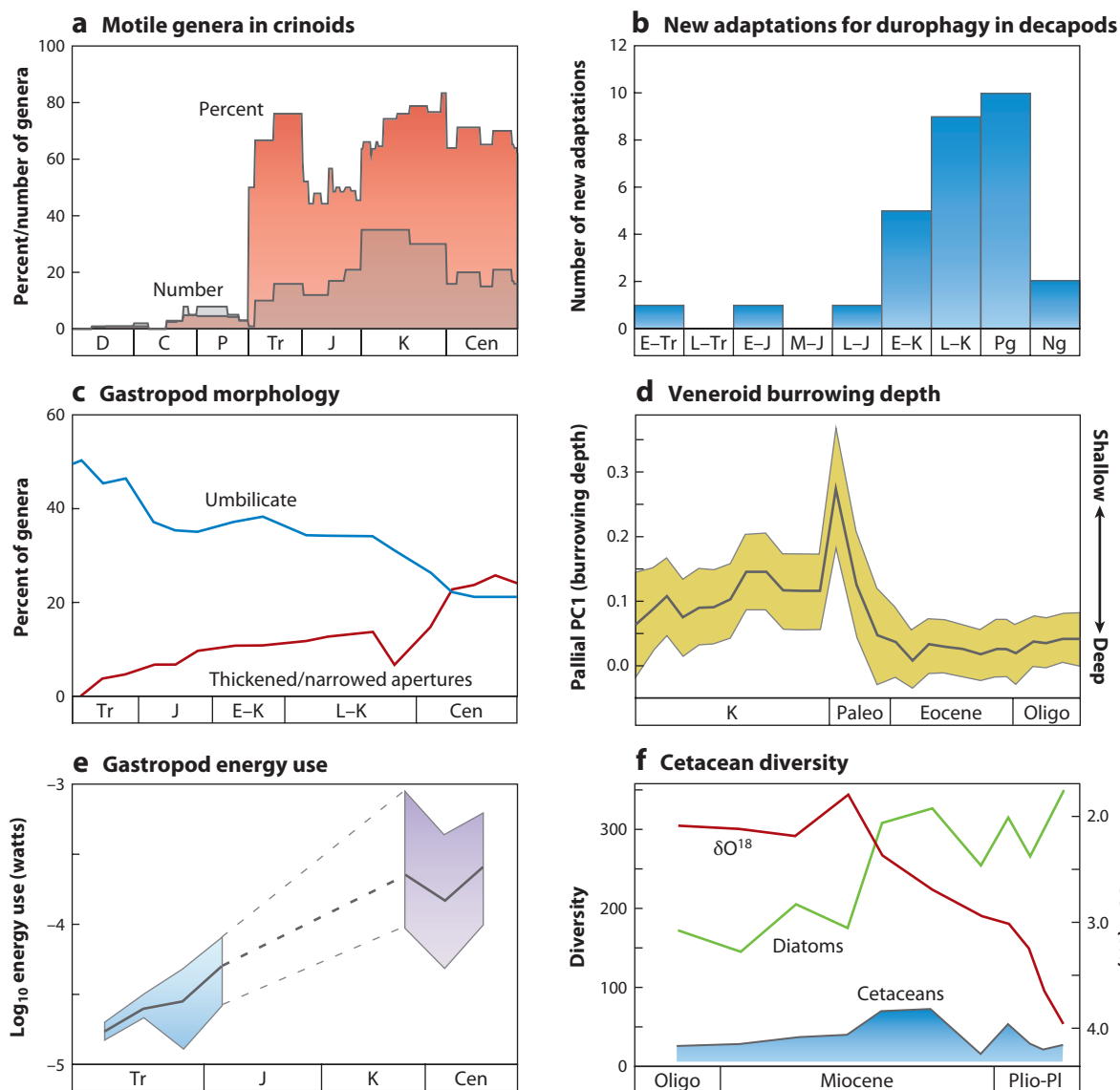


Figure 5

Paleocologic changes in the Mesozoic and Cenozoic. (a) Percentage and number of crinoid genera inferred to be motile (adapted from Baumiller & Messing 2007). (b) Number of new adaptations per time bin for durophagous predation in decapod crustaceans (data from Schweitzer & Feldmann 2010). (c) Trends in gastropod morphology, with predation-resistant morphologies increasing and predation-susceptible morphologies decreasing through time (adapted from Vermeij 1997). (d) Burrowing depth in veneroid bivalves, as inferred from pallial sinus depth (adapted from Lockwood 2004, with permission from the Paleontological Society). Mean \pm standard error. (e) Energy use by gastropod assemblages through the Mesozoic and Cenozoic (adapted from Finnegan et al. 2011). Medians and 95% quantiles. (f) Cetacean genus diversity, diatom species diversity, and δO^{18} , a proxy for temperature (adapted from Marx & Uhen 2010; reprinted with permission from AAAS). Cetacean diversity could be explained statistically by the other two variables. Timescale abbreviations: E, Early; M, Middle; L, Late; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Cen, Cenozoic; Pg, Paleogene; Ng, Neogene; Paleo, Paleocene; Oligo, Oligocene; and Plio-Pl, Pliocene-Pleistocene.

The singular impact of the Permian extinction on marine ecology and evolution must lie in both its magnitude and its ecological selectivity. Stationary epifauna constituted well over half of the fossilized marine genera in the Permian (**Figure 3e**), but their diversity plunged as a result of the extinction, and they never regained dominance. Instead of reradiating, the Late Paleozoic fauna was hit again in the end-Triassic extinction and petered out in the Jurassic (**Figure 2**). Similarly, the epifaunal components of the Early Paleozoic fauna (fauna 6) suffered at the end of the Permian, and the end-Triassic event virtually eliminated the rest (**Figure 2b**). The faunas that survived the Permian-Triassic extinction relatively unscathed (faunas 9–11) were considerably more diverse in ecology than the Late Paleozoic fauna, each representing multiple tiers and feeding types. They suffered little to no extinction in absolute terms [i.e., number of genera (**Figure 3a**)] and surged in proportional diversity in the Early Triassic due to the elimination of taxa in the Early and Late Paleozoic faunas (**Figure 2**). Thus, the extinction acted as a filter that helped establish the ecological disparity of the modern biota.

Of the faunas that survived the Permian extinction, the Phanerozoic fauna (fauna 9) was the most diverse in the Late Permian and thus constituted the bulk of the survivor fauna in the Triassic (**Figure 2**). It had radiated throughout the Paleozoic alongside the Late Paleozoic fauna and thus represents (in a sense) the remnant of the Late Paleozoic biota that was resistant to the effects of the Permian extinction. However, after the Permian-Triassic extinction, the Phanerozoic fauna did not continue to radiate substantially; rather, it maintained relatively constant absolute diversity and declined in proportional diversity as other groups radiated (**Figures 2 and 3a**).

The Phanerozoic fauna includes several groups of sponges, brachiopods, bivalves, and gastropods, as well as ammonoids, polychaetes, ophiroids, and holothuroids. A couple of these groups could be revised taxonomically (e.g., “archaeogastropoda”) or split to reveal turnover (ammonoids); some also may have a poor record of body fossils (e.g., polychaetes, holothuroids); but many are morphologically/ecologically conservative (e.g., nuculoid and solemyoid bivalves: Levinton & Bambach 1975). These groups apparently evolved successful ecological strategies in the Paleozoic (e.g., palp-probiscide deposit feeding in nuculoid bivalves) and were capable of coping with the increasing disturbance that characterized the Mesozoic and Cenozoic through motility or some other attribute (e.g., secure attachment in pteroid bivalves and rhynchonellid and terebratulid brachiopods).

The Mesozoic and Mesozoic-Cenozoic faunas, which were not abundant in the Paleozoic, diversified in the extinction’s aftermath (**Figure 2**). Members of the Mesozoic fauna either went extinct at the end of the Cretaceous or did not continue to radiate in the Cenozoic (e.g., Scleractinia), thus constituting a decreasing proportion of the biota (**Figure 2**). Although the Hippuritoida did not cluster with the Mesozoic (or any other) fauna, the importance of rudistid reefs in the Cretaceous and their extinction near the end of the Mesozoic made their placement in fauna 10 logical. The Mesozoic fauna declined proportionally during the late Mesozoic and Cenozoic in much the same way as the Phanerozoic fauna, and indeed many members of our Mesozoic fauna were included by Sepkoski (1981) in his Paleozoic fauna (e.g., scleractinian corals, thecideide brachiopods, coleoid cephalopods, and articulate crinoids). In fact, some of these taxa belong in clades with “Paleozoic” taxa but are split off in this traditional taxonomy due to significant morphologic evolution, leaving their Paleozoic relatives in paraphyletic groups (e.g., thecideide brachiopods, articulate crinoids). However, these particular groups arguably have adaptations for coping with higher levels of disturbance in the Mesozoic [e.g., encrusting in the corals and thecideides, motility in the crinoids (see Bambach 1985 for full discussion)].

Early Triassic ecosystems were depauperate in both taxonomic and ecologic diversity. The depth of infaunal tiering and intensity of bioturbation were reduced following the end-Permian extinction (**Figure 3b**; Twitchett 1999, Pruss et al. 2005). The extinction also reduced the height

and complexity of epifaunal tiering (Twitchett 1999); for example, crinoids suffered badly, and reefs were eliminated entirely. In many locations around the world, stromatolites and other indicators of microbial growth proliferated after the Permian-Triassic extinction (Pruss et al. 2005, Payne et al. 2006), suggesting that grazing and sediment disturbance by animals decreased dramatically to levels rarely seen since the Cambrian. Indeed, Payne et al. (2006) found that in South China the density of shells dropped across the Permian-Triassic boundary by up to an order of magnitude.

The wake of the Permian extinction was a time of great change (Vermeij 2008, Baumiller et al. 2010). For most of the Paleozoic, predators constituted approximately 15% of the genera in the marine fauna, but after a spike in the Triassic driven by ammonoids (Brayard et al. 2009), they made up approximately 20% of genera during the Mesozoic (**Figure 3c**). Groups that include predators that radiated at this time include the marine reptiles, coleoids, and the microcarnivorous scleractinian corals (all in the Mesozoic fauna), as well as the malacostracans, certain gastropods, chondrichthyans, and actinopterygians (all in the Mesozoic-Cenozoic fauna) (**Figure 2c**). The infauna also increased in diversity, abundance, and effect on sediments beginning in the early Mesozoic (**Figures 2b** and **3b,d,e**). For example, veneroid and myoid bivalves evolved siphons in the early Mesozoic and invaded the deep infauna (Stanley 1968). The mobile epifauna also began to increase proportionally (**Figure 3e**). The relative diversification rates of the Mesozoic-Cenozoic and Phanerozoic faunas reversed as a result of the extinction, indicating some sort of major ecological change that affected evolution. The Phanerozoic fauna switched from increasing as a proportion of the fauna in the late Paleozoic to decreasing as a proportion in the Triassic, whereas the Mesozoic-Cenozoic fauna was not diversifying relative to the rest of the fauna in the late Paleozoic, but began to do so in the Triassic.

Baumiller & Messing (2007) and Baumiller et al. (2010) presented a striking example of ecological evolution in the Triassic. A few late Paleozoic crinoids may have had some measure of motility, but they were outnumbered vastly by those that show no evidence of motility. Crinoids experienced a severe bottleneck at the Permian-Triassic extinction, and motile forms radiated preferentially in the Middle-Late Triassic and have dominated crinoid diversity ever since (**Figure 5a**). Baumiller et al. (2010) linked this trend to the diversification and evolution of improved predatory abilities by cidaroid echinoids.

Late Mesozoic-Cenozoic

The Mesozoic-Cenozoic fauna increased substantially as a proportion of the marine fauna in the Cretaceous and early Cenozoic, and the Cenozoic fauna (consisting of neogastropods and mammals) radiated in the Late Cretaceous and Cenozoic (**Figure 2**). These radiations drove several shifts in the ecologic balance of the global marine fauna. Many members of the Mesozoic-Cenozoic fauna were infaunal in whole or part (**Figure 2b**), and the proportion of infauna in the global biota increased (**Figure 3e**). Some of these taxa, such as myoids and veneroids, include deep-burrowing members. The proportion of stationary epifauna declined further (**Figure 3e**), especially members of the Phanerozoic fauna (**Figure 2b**). The mobile epifauna expanded strongly in the Cenozoic (**Figure 3e**), driven by the neogastropod radiation (see mobile epifaunal taxon in the Cenozoic fauna in **Figure 2b**). Interestingly, the proportion of pelagic taxa did not change (**Figure 3e**), but ammonites and most marine reptiles went extinct at the end of the Cretaceous and were replaced numerically by fish and mammals (see pelagic taxa in faunas 9–12 in **Figure 2b**). Because most infauna and pelagic taxa are motile, the proportion of motile taxa in the global biota was quite substantial by the Neogene (**Figure 3e**).

An intensification of predation is well known in the later Mesozoic and Cenozoic (the Mesozoic Marine Revolution) (Stanley 1974; Vermeij 1977, 1987; Walker & Brett 2002; Harper 2003). In

Stromatolite:
layered, accretionary mound typically formed by the trapping, binding, and cementation of sedimentary particles by microbial mats

the global data shown here, the proportion of predators in the marine fauna did not change until after the Cretaceous-Tertiary boundary, when the neogastropod radiation picked up steam and other taxa that include predators radiated as well (see taxa in the Mesozoic-Cenozoic fauna in **Figure 2c**). Other sources of information indicate that predation intensity increased in the late Mesozoic as well as in the Cenozoic. Drilled shells, evidence of predation primarily by muricid and naticid gastropods at this time, increased in frequency in the Late Cretaceous and Paleogene (**Figure 3c**; Kelley & Hansen 2003, Huntley & Kowalewski 2007). Furthermore, the number of groups of shell-crushing predators increased in the Cretaceous and Cenozoic (Vermeij 1987); as an example, **Figure 5b** shows the timing of appearance of new adaptations for crushing in decapod crustaceans (Schweitzer & Feldmann 2010), and **Figure 1f** shows a modern durophagous bat ray. Antipredatory shell morphologies increased through the Mesozoic and into the Cenozoic, whereas weaker, umbilicate shells declined in frequency (e.g., **Figure 5c**; Vermeij 1987). After the Cretaceous, stalked crinoids were found primarily in the deep sea, which has been attributed to high predation intensity in shallow water (Meyer & Macurda 1977, Bottjer & Jablonski 1988, Oji 1996). High epifaunal tiers in shallow shelf environments disappeared as a result (**Figure 3b**). Grazing intensity increased as well (Steneck 1983).

The end-Cretaceous extinction did not rearrange the marine biosphere in the manner of the end-Permian event, but it certainly had some effects. As mentioned above, the relative diversity of predators and motile epifauna shot up during the recovery from the extinction (**Figure 3c,e**), driven by the diversification of the Cenozoic fauna (**Figure 2**), and infaunal taxa such as the veneroid bivalves radiated (**Figure 3e**). In fact, the average depth of burrowing increased even within the veneroids—after a decrease in average burrowing depth as a result of the Cretaceous extinction, deep burrowing forms radiated strongly during the recovery (**Figure 5d**; Lockwood 2004).

Increases in motility and sediment disturbance during the Mesozoic and Cenozoic had negative impacts on some ecological lifestyles, as in earlier times, such as the Cambrian. Reclining animals, which lie unattached and immobile on the seafloor, were common in the Paleozoic (e.g., brachiopods) and in the Mesozoic (e.g., the oyster *Exogyra*). This lifestyle is virtually absent today (Thayer 1979)—most animals are attached or have some method of reorienting if disturbed. In a classic experiment, Labarbera (1981) placed models of Mesozoic oysters on the modern seafloor, and indeed many were flipped over by the activities of motile animals (which would have presumably killed a real animal) or attacked by predators.

Increases in high-energy taxa such as predators, burrowers, and other motile forms, as well as increases in body size, have led to suggestions that the energetics of the global marine biosphere increased at this time (e.g., Vermeij 1987, 1995; Bambach 1993, 1999). Finnegan et al. (2011) tested this hypothesis using Mesozoic and Cenozoic assemblages of gastropods and estimated that energy use increased by at least 150% and perhaps more (**Figure 5e**). Increased energy use by animals could be linked to increased nutrients from land, related to the spread of angiosperms (Bambach 1999); increased nutrients from submarine volcanism (Vermeij 1995); and/or the radiation of several groups of phytoplankton (diatoms, calcareous nannoplankton, and dinoflagellates) (Falkowski et al. 2004, Knoll et al. 2007b). The link between primary production and diversity was tested explicitly for cetaceans by Marx & Uhen (2010), who found that cetacean diversity could be explained by a combination of diatom diversity and temperature (**Figure 5f**).

DISCUSSION

A suite of changes has swept marine metazoan ecosystems from the Neoproterozoic to the present, with increases in (a) predation, (b) motility, (c) infaunality, (d) biological disturbance, and (e) energy use. These parameters may not have changed constantly or in unison, but evidence shows a general

tendency of increase. Mass extinctions temporarily impeded or reversed some of these trends (e.g., a reduction in bioturbation after the Permian extinction), but the trends resumed or even accelerated during recovery intervals. These changes often are discussed as discrete phenomena (various revolutions), but they appear to be segments of one or a few paleoecologic megatrends that span the history of marine metazoa, and this raises many interesting questions.

Causality

What, if anything, drove these trends in the marine biosphere? We reference numerous causal explanations throughout this review; most paleontologists would readily accept that increased predation likely drove some increases in defensive morphologies, motility (e.g., escape responses), and infaunality of suspension feeders. Likewise, animals that cause disturbance probably caused the decline of animals unable to cope with high disturbance and set the stage for the evolution or expansion of other taxa.¹ These explanations would qualify many of these trends as driven or active, *sensu* McShea (1994).

However, what was the ultimate driver of all these ecological changes? If increased predation and motility (i.e., disturbance) drove other ecological trends, why did predation and motility change? It is certainly plausible that some change in the environment (biotic or abiotic) played a role in these trends. For example, increased primary production or higher oxygen levels could permit more energetic ecosystems with greater proportions of motile and predatory animals. It is even possible that these trends were self-reinforcing, in that increases in planktonic and burrowing animals increased the recycling of nutrients, which allowed increased primary productivity (e.g., Thayer 1983, Martin 1996, Vermeij 1999). Vermeij (1999) has even argued that natural selection intrinsically favors high-energy forms. However, it could also be argued that these paleoecologic megatrends can be explained, at least on some level, by passive expansion from Ediacaran ecosystems characterized by low predation, biological disturbance, and energy use (see similar arguments in Huntley & Kowalewski 2007). Data specifically collated to test models of causality are still needed.

Local Abundances and Ecological Complexity

Bush et al. (2007) and Novack-Gottshall (2007) examined changes through time in the local relative abundances of ecological lifestyles (i.e., within paleocommunities). Bush et al. (2007) used the ecospace categorization shown in **Figure 1**, whereas Novack-Gottshall (2007) used his more detailed ecospace model. Both studies revealed that global trends can be observed easily at the local level: From the Paleozoic to the Cenozoic, there was an increase in the relative abundance of infaunal animals, motile and facultatively motile animals, and predators. Novack-Gottshall (2007) also found an increase in animals that use other animals and structures as microhabitats.

These studies revealed several other interesting patterns. For example, although the global diversity of ecological lifestyles approximately doubled between the Late Ordovician and late

¹ Statistical tests of causality have not been simple, and some efforts have foundered on multiple fronts (Dietl & Vermeij 2006; Madin et al. 2006a,b; Roopnarine et al. 2006; Bush et al. 2007; although see Marx & Uhen 2010 for an interesting example). Much of the data that we and others have shown is global in scale, but many of the interactions of interest occur at local to regional scales, and some argue that the relationships among variables are best examined at those scales (e.g., Vermeij 2008). However, local and regional studies are more likely to suffer from variations in the quality of the fossil record, or other variations that are simply difficult to explain (e.g., Kelley & Hansen 2003, Leighton 2003). Trends may have several causes, but some variables are difficult to measure (e.g., the intensity of many types of predation). Given all the evidence that has been gathered, however, most paleontologists would accept the importance of factors such as predation and disturbance in the history of life, although all details are not understood.

COMPLEXITY

Complexity can be defined as a “function of the number of different types of parts or interactions” that characterize a system (McShea 1996). In paleobiology, the concept has been applied most often to morphology, but it pertains equally well to ecosystems. A complex ecosystem is characterized by organisms that perform many functions and by numerous types of ecological interactions. In contrast, organisms in a simple ecosystem would fulfill fewer ecological roles and would interact in fewer ways. **Figure 1a–d** illustrates an increase in ecological complexity from the Ediacaran Period to the Recent, as represented by the number of modes of life found in the global marine fauna. The frequency of various interactions among organisms also appears to have increased through time (e.g., predation and disturbance; **Figures 3–5**).

Cenozoic (**Figure 1d**), the number of lifestyles living in soft-sediment habitats has not increased substantially since the middle Paleozoic (Bush et al. 2007, Novack-Gottshall 2007). However, Novack-Gottshall (2007) showed that the lifestyles found in this habitat were ecologically more disparate in the Cenozoic than in the Paleozoic; that is, many of the lifestyles in this habitat in the Paleozoic were variations on a few themes (e.g., various types of epifaunal suspension feeders). Bush et al. (2007) also found that Paleozoic collections from soft-sediment habitats tended to be dominated by individuals belonging to a few common ecological lifestyles, whereas lifestyles in Cenozoic assemblages were more evenly distributed (e.g., see data for suspension feeders in **Figure 3f**). Taphonomic biases could not account completely for differences in these distributions.

Both observations speak to an increase in ecological complexity at the local level (see sidebar, Complexity). The biological landscape in the Paleozoic was relatively uniform—several ecological lifestyles dominated, and many ecological lifestyles were similar in many properties. By the Cenozoic, more lifestyles were relatively common, and these lifestyles were more disparate in their ecology. Thus, an animal in the modern oceans is likely to be involved in more diverse types of biotic interactions compared with one in the Paleozoic. Increased within-habitat diversity is likely to exacerbate this trend (Bambach 1977, Powell & Kowalewski 2002, Bush & Bambach 2004, Alroy et al. 2008; see also Wagner et al. 2006).

The increase in the disparity and evenness of ecological lifestyles may reflect a reorganization of the ecological forces directing evolution within a habitat. Early in metazoan history, predation and disturbance were less intense, and in general, animals displayed fewer morphologies and behaviors adapted to resist them. For example, a high proportion of suspension feeders were nonmotile and epifaunal (**Figure 3f**; Bush et al. 2007). This lifestyle is efficient, in that food is easily accessible and energy is not wasted on moving. With the increase in predation and disturbance, life became increasingly complex, in that most animals had to adequately perform additional functions to survive and reproduce (i.e., avoid or cope with predation and disturbance). The increased evenness and disparity of lifestyles may reflect that many combinations of traits [e.g., motility, burrowing (**Figure 3f**)] are possible that balance these competing needs, whereas a narrower range of ecologic lifestyles was best adapted to conditions in the Paleozoic. This idea derives from similar logic that Niklas (1994) and Marshall (2006) developed and applied to plant and animal morphology, respectively.

Role of Mass Extinctions

The most obvious effect of mass extinctions on long-term ecological trends is, of course, the elimination of taxa that thereafter play no role in the ecosystem. Selective extinctions alter the

representation of different ecological lifestyles, the most obvious example being the selective elimination of nonmotile, epifaunal suspension feeders at the end of the Permian (**Figure 2**). The residual biota was enhanced significantly in more active lifestyles.

The recovery intervals after mass extinctions may be equally critical in shaping the ecology of the biosphere. Since the Ordovician Radiation, the most sustained changes in the proportion of predators and motility categories in the marine biota occurred after the Permian and Cretaceous extinctions, and the recovery intervals were key in establishing these changes (**Figure 3c,e**; Bambach et al. 2002). [One caveat is necessary: The change in proportional predator diversity between the Cretaceous and Cenozoic was driven largely by the radiation of neogastropods, and this radiation began in the Cretaceous, so it is difficult to say what would have happened in the absence of the extinction (see **Figure 2**).] The radiations of motile crinoids in the Triassic (**Figure 5a**; Baumiller & Messing 2007, Baumiller et al. 2010) and deep-burrowing veneroids in the early Cenozoic (**Figure 5d**; Lockwood 2004) are specific case studies that support a role for postextinction intervals in reorganizing marine ecology.

We have a great deal to learn about how and why ecologic changes occurred during recoveries from extinctions; presumably, ecological interactions changed in strength in the postextinction environment, altering the direction of evolution. However, sorting out which interactions and processes were most important may not be a trivial task: Candidates include competition, predation, and disturbance (e.g., Stanley 2008). Alternatively, the persistence of unusual environmental conditions related to a mass extinction could favor the evolution of certain lifestyles. In any case, the largest mass extinctions significantly changed the ecological context in which evolution occurred, and this is reflected by changes in life habits during recovery intervals. A better understanding of these dynamics should be a priority in paleoecology.

The mass extinctions with large ecological impact are associated with increases in motility and predation (**Figure 3c,e**). Is this coincidental, or are certain ecological lifestyles better able to adapt and diversify in the postextinction world? Would predation and motility have increased anyway given enough time, or do extinctions place a highly contingent imprint on Earth's biota (cf. Sepkoski 1984)?

What Makes a Successful Clade?

Are there any ecological reasons why some taxa/clades diversify, or at least persist, while others go extinct? As mentioned above, Vermeij (1999) has argued that energy-intensive forms are favored through time by natural selection. These forms certainly appear to have increased through time, although other causal hypotheses have been advanced as well (e.g., a change in primary production). Bambach (1985) argued that taxonomic classes increased in diversity only if they evolved new features that permitted the invasion of ecospace previously unexploited by members of the class. Classes that only maintained their diversity over long intervals of geological time did not evolve new features that opened the way to unoccupied ecospace, but they often displayed internal taxonomic turnover that enabled survival under changed circumstances—new orders within these classes generally evolved new abilities to cope with increasing disturbance levels, and these groups replaced the diversity lost by less-resistant taxa as they waned.

If there is a general theme to be perceived in the trends discussed here, it is an increase through time in animals' ability to control their external and internal conditions. The ability to move (or if not, to attach robustly at least) permits control over interactions with the biotic and abiotic environment. An associated characteristic is the ability to actively manipulate the environment through the use of appendages or other morphologic features; many successful clades

have morphologies that have been exapted (Gould & Vrba 1982) for many ways of interacting with the environment (e.g., crustaceans, gastropods, bivalves, vertebrates, and echinoids). The abilities to control movement and manipulate the environment are critical in coping with a wide range of difficulties, including predation and disturbance. The ability to control physiology has been equally important; for example, in the end-Permian extinction, animals that had greater physiological control over the precipitation of calcium carbonate fared better than those that did not (Knoll et al. 2007a). In fact, organisms whose bodies were well buffered against physiological (i.e., chemical) stress constituted approximately 30% of genera in the Paleozoic, and this percentage rose to almost 70% by the late Cenozoic (Bambach et al. 2002). The ability to control the environment and one's internal state has evidently given some organisms the flexibility to cope with adverse conditions and to evolve new ecological strategies.

Another factor related to the long-term success of a clade is its rate of origination and extinction [the two are closely balanced (e.g., Stanley 2007)]. Taxa with high rates are highly volatile (Gilinsky 1994), and they tend to diversify rapidly, but they go extinct quickly as well, even if only by stochastic processes. These taxa typically went extinct early in metazoan history and belong to the low-numbered faunas in **Figure 2**. High volatility can be imparted by a small geographic range, small number of species, a variety of population-level parameters, and perhaps other factors (Stanley 2007, Payne & Finnegan 2007). If evolutionary volatility is an intrinsic property of a clade, then evolutionary turnover results in part from stochastic, rather than ecological (as discussed here), effects. Some taxa just may have lacked the macroevolutionary characteristics to persist for vast lengths of geological time.

Exceptions to Megatrends

We describe these trends as general tendencies because, although they appear to describe the history of marine metazoa well, there are a few exceptions. There was an increase in the proportional diversity of motile animals in the Cambrian (largely trilobites), which was then reversed as stationary epifauna radiated in the Ordovician Radiation. If there is a tendency toward motility, why this reversal? In all likelihood, the structure of metazoan ecosystems was not well established until the Ordovician Radiation. Suspension feeders typically outnumber deposit feeders in the global biota, and in the low-disturbance world of the Early Paleozoic, many of them had no need for motility. However, the extinction of archaeocyaths left this lifestyle underpopulated, and it was a while before it was abundantly reoccupied (see Pruss et al. 2010 for a geobiological explanation). Deposit feeders may have been unusually abundant in the meantime (**Figure 2**).

The late Paleozoic is also worthy of note. Stationary epifaunal groups such as brachiopods, bryozoans, and crinoids radiated with great success at this time and occupied their greatest share ever of the global biota (**Figure 3e**). The Mesozoic-Cenozoic fauna, which contained a diverse array of motile taxa, actually declined as a share of the global biota in the late Paleozoic (**Figure 2**). Only once the Permian extinction eliminated many stationary taxa did dominance shift to more active forms. It is also perhaps notable that traces of predation such as drill holes and healed predation scars peaked in the middle Paleozoic and then declined (**Figure 3c**), although more data are needed. It is possible that increases in spinosity and shell thickness during the Mid-Paleozoic Marine Revolution (e.g., **Figure 4e,f**) were sufficient to deal with levels of disturbance and predation in the late Paleozoic, such that stationary epifauna continued to be successful. The increase in their diversity also may reflect the reestablishment of large-scale reefs. In any case, the success of stationary epifauna in the late Paleozoic reinforces the importance of the Permian extinction in reorganizing marine ecology.

The Future

Given the slowdown in rates of origination and extinction toward the present at all levels (lower taxa, higher taxa, and faunas), the oceans in the future probably will be populated by taxa similar to those that dominate today (e.g., bivalves, gastropods, fish, crustaceans, gymnolaemata). That is, there is no indication that the Cenozoic and Mesozoic-Cenozoic faunas are going to be replaced soon given the slow pace of change currently observed (**Figure 2**). However, these taxa are likely to explore new ecological lifestyles as time passes. Of course, a selective mass extinction could thin the fauna into victims and survivors.

SUMMARY POINTS

1. Increased predation, motility, biological disturbance, energy use, infaunality, and ecological complexity have transformed marine ecosystems since the late Proterozoic. On average, animals have gained greater control over their internal physiology and their external physical environment. These trends are not unrelated and can perhaps be viewed as part of the same transformation, although change has not been continuous and different clades have been affected at different times.
2. Increased predation and disturbance plausibly drove numerous paleoecologic trends, but the causes of increased predation and disturbance merit further examination. Could these simply be passive trends away from early metazoan ecosystems that were characterized by low disturbance and predation? Or must they be explained by changes in the environment, such as increased primary production?
3. Every organism is limited by its physiological tolerances, so abiotic factors may explain many trends in diversity and ecology. The relative contributions of abiotic and biotic factors on ecologic history require further investigation.
4. Mass extinctions sometimes set back ecological trends (e.g., reductions in tiering, biomass), but only temporarily. At other times, extinctions appear to hasten ecological trends (e.g., the elimination of many nonmotile epifauna in the Permian extinction). The recoveries from large mass extinctions appear to be times of rapid ecological change as well, although the exact mechanisms involved need to be better elucidated.

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LITERATURE CITED

- Adrain JM, Fortey RA, Westrop SR. 1998. Post-Cambrian trilobite diversity and evolutionary faunas. *Science* 280:1922–25
- Alexander RR. 1989. Influence of valve geometry, ornamentation, and microstructure on fractures in Late Ordovician brachiopods. *Lethaia* 22:133–47

An early discussion of the ecospace concept.

- Alroy J, Aberhan M, Bottjer DJ, Foote M, Fürsich FT, et al. 2008. Phanerozoic trends in the global diversity of marine invertebrates. *Science* 321:97–100
- Ausich WI, Bottjer DJ. 1982. Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. *Science* 216:173–74
- Ausich WI, Bottjer DJ. 2001. Sessile invertebrates. In *Palaeobiology II*, ed. DEG Briggs, PR Crowther, pp. 384–86. Oxford: Blackwell
- Babcock LE. 2003. Trilobites in Paleozoic predator-prey systems, and their role in reorganization of early Paleozoic ecosystems. See Kelley et al. 2003, pp. 55–92
- Bambach RK. 1977. Species richness in marine benthic habitats through the Phanerozoic. *Paleobiology* 3:152–67
- Bambach RK. 1983. Ecospace utilization and guilds in marine communities through the Phanerozoic. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. MJS Tevesz, PL McCall, pp. 719–46. New York: Plenum**
- Bambach RK. 1985. Classes and adaptive variety: the ecology of diversification in marine faunas through the Phanerozoic. In *Phanerozoic Diversity Patterns*, ed. JW Valentine, pp. 191–253. Princeton, NJ: Princeton Univ. Press
- Bambach RK. 1993. Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology* 19:372–97
- Bambach RK. 1999. Energetics in the global marine fauna: a connection between terrestrial diversification and change in the marine biosphere. *Geobios* 32:131–44
- Bambach RK, Bush AM, Erwin DH. 2007. Autecology and the filling of ecospace: key metazoan radiations. *Palaeontology* 50:1–22
- Bambach RK, Knoll AH, Sepkoski JJ Jr. 2002. Anatomical and ecological constraints on Phanerozoic animal diversity in the marine realm. *Proc. Natl. Acad. Sci. USA* 99:6854–59
- Bambach RK, Knoll AH, Wang S. 2004. Origination, extinction, and mass depletions of marine diversity. *Paleobiology* 30:522–42
- Baumiller TK. 1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. *Palaeontology* 33:743–48
- Baumiller TK, Gahn FJ. 2002. Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interaction. See Kowalewski & Kelley 2002, pp. 195–209
- Baumiller TK, Gahn FJ. 2004. Testing predator-driven evolution with Paleozoic crinoid arm regeneration. *Science* 305:1453–55
- Baumiller TK, Messing CG. 2007. Stalked crinoid locomotion, and its ecological and evolutionary implications. *Palaeontol. Electron.* 10:10.1.2A
- Baumiller TK, Salamon MA, Gorzelak P, Mooi R, Messing CG, Gahn FJ. 2010. Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. *Proc. Natl. Acad. Sci. USA* 107:5893–96
- Bengtson S. 2002. Origins and early evolution of predation. See Kowalewski & Kelley 2002, pp. 289–317
- Bengtson S, Zhao Y. 1992. Predatorial borings in late Precambrian mineralized exoskeletons. *Science* 257:367–69
- Berke SK. 2010. Functional groups of ecosystem engineers: a proposed classification with comments on current issues. *Integr. Comp. Biol.* 50:147–57
- Bottjer DJ, Hagadorn JW, Dornbos SQ. 2000. The Cambrian substrate revolution. *GSA Today* 10:1–7
- Bottjer DJ, Jablonski D. 1988. Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. *Palaios* 3:540–60
- Bouchet P, Rocroi JP, eds. 2005. Classification and nomenclator of gastropod families. *Malacologia* 47:1–397
- Brayard A, Escarguel G, Bucher H, Monnet C, Brühwiler T, et al. 2009. Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. *Science* 325:1118–21
- Brett CE. 2003. Durophagous predation in Paleozoic marine benthic assemblages. See Kelley et al. 2003, pp. 401–32

- Brett CE, Walker SE. 2002. Predators and predation in Paleozoic marine environments. See Kowalewski & Kelley 2002, pp. 93–118
- Briggs DEK, Erwin DH, Collier FJ. 1994. *The Fossils of the Burgess Shale*. Washington, DC: Smithsonian Inst.
- Bush AM, Bambach RK. 2004. Did alpha diversity increase through the Phanerozoic? Lifting the veils of taphonomic, latitudinal, and environmental biases. *J. Geol.* 112:625–42
- Bush AM, Bambach RK, Daley GM. 2007. Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic. *Paleobiology* 33:76–97
- Bush AM, Bambach RK, Erwin DH. 2011. Ecospace utilization during the Ediacaran radiation and the Cambrian eco-explosion. In *Quantifying the Evolution of Early Life: Numerical Approaches to the Evaluation of Fossils and Ancient Ecosystems*, ed. M Laflamme, JD Schiffbauer, SQ Dornbos. Berlin: Springer. In press
- Clapham ME, Narbonne GM. 2002. Ediacaran epifaunal tiering. *Geology* 30:627–30
- Clifton HE. 1971. Orientation of empty pelecypod shells and shell fragments in quiet water. *J. Sediment. Res.* 41:671–82
- Copper P. 2002. Reef development at the Frasnian/Famennian mass extinction boundary. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 181:27–65
- Dahl TW, Hammarlund EU, Anbar AD, Bond DPG, Gill BC, et al. 2010. Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *Proc. Natl. Acad. Sci. USA* 107:17911–15
- Dietl GP, Vermeij GJ. 2006. Comment on “Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates.” *Science* 314:925e
- Dornbos SQ. 2006. Evolutionary palaeoecology of early epifaunal echinoderms: response to increasing bioturbation levels during the Cambrian radiation. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 237:225–39
- Droser ML, Bottjer DJ. 1989. Ordovician increase in extent and depth of bioturbation: implications for understanding early Phanerozoic ecospace utilization. *Geology* 17:850–52
- Droser ML, Jensen S, Gehling JG. 2002. Trace fossils and substrates of the terminal Proterozoic-Cambrian transition: implications for the record of early bilaterians and sediment mixing. *Proc. Natl. Acad. Sci. USA* 99:12572–76
- Dunne JA, Williams RJ, Martinez ND, Wood RA, Erwin DH. 2008. Compilation and network analysis of Cambrian food webs. *PLoS Biol.* 6:e102
- Dzik J. 2003. Anatomical information content in the Ediacaran fossils and their possible zoological affinities. *Integr. Comp. Biol.* 43:114–26
- Falkowski PG, Katz ME, Knoll AH, Quigg A, Raven JA, et al. 2004. The evolution of modern eukaryotic phytoplankton. *Science* 305:354–60
- Fedonkin MA, Simonetta A, Ivantsov AY. 2007. New data on *Kimberella*, the Vendian mollusc-like organism (White Sea region, Russia): paleontological and evolutionary implications. In *The Rise and Fall of the Ediacaran Biota*, ed. P Vickers-Rich, P Komarower, pp. 157–79. London: Geol. Soc.
- Finnegan S, Droser ML. 2008. Body size, energetics, and the Ordovician restructuring of marine ecosystems. *Paleobiology* 34:342–59
- Finnegan S, McClain CM, Kosnik MA, Payne JL. 2011. Escargot through time: an energetic comparison of marine gastropod assemblages before and after the Mesozoic Marine Revolution. *Paleobiology*. In press
- Fortey RA, Owens RM. 1999. Feeding habits in trilobites. *Palaeontology* 42:429–65
- Gehling JG, Droser ML, Jensen SR, Runnegar BN. 2005. Ediacara organisms: relating form to function. In *Evolving Form and Function: Fossils and Development*, ed. DEG Briggs, pp. 43–66. New Haven, CT: Yale Peabody Mus. Nat. Hist.
- Gilinsky NL. 1994. Volatility and the Phanerozoic decline of background extinction intensity. *Paleobiology* 20:445–58
- Gould SJ, Vrba ES. 1982. Exaptation: a missing term in the science of form. *Paleobiology* 8:4–15
- Grazhdankin D, Seilacher A. 2002. Underground Vendobionta from Namibia. *Palaeontology* 45:57–78
- Grotzinger JP, Watters WA, Knoll AH. 2000. Calcified metazoans in thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia. *Paleobiology* 26:334–59

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- Harper EM. 2003. The Mesozoic marine revolution. See Kelley et al. 2003, pp. 433–55
- Hendy AJW, Aberhan M, Alroy J, Clapham ME, Kiessling W, Lin J-P. 2009. A 600 million year record of ecological diversification. *Geol. Soc. Am. Abstr. Prog.* 41:508
- Hou X-G, Adridge RJ, Bergström J, Siveter DJ, Siveter DJ, Feng X-H. 2004. *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life*. Malden, MA: Blackwell Sci.
- House MR. 2002. Strength, timing, setting and cause of mid-Palaeozoic extinctions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 181:5–25
- Hua H, Pratt BR, Zhang L-Y. 2003. Borings in *Cloudina* shells: complex predator-prey dynamics in the terminal Neoproterozoic. *Palaiois* 18:454–59
- Huntley JW, Kowalewski M. 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proc. Natl. Acad. Sci. USA* 104:15006–10
- Ivantsov AY, Malakhovskaya YE. 2002. Giant traces of Vendian animals. *Dokl. Earth Sci.* 385A:618–22
- Kelley PH, Hansen TA. 2003. The fossil record of drilling predation on bivalves and gastropods. See Kelley et al. 2003, pp. 113–39
- Kelley PH, Kowalewski M, Hansen TA, eds. 2003. *Predator-Prey Interactions in the Fossil Record*. New York: Plenum/Kluwer
- Knoll AH, Bambach RK, Payne JL, Pruss S, Fischer WW. 2007a. Paleophysiology and end-Permian mass extinction. *Earth Planet. Sci. Lett.* 256:295–313
- Knoll AH, Summons RE, Waldbauer JR, Zumbege JE. 2007b. The geological succession of primary producers in the oceans. In *The Evolution of Primary Producers in the Sea*, ed. P Falkowski, AH Knoll, pp. 133–63. Burlington, MA: Elsevier
- Kosnik MA, Jablonski D, Lockwood R, Novack-Gottshall PM. 2006. Quantifying molluscan body size in evolutionary and ecological analyses: maximizing the return on data-collection efforts. *Palaiois* 21:588–97
- Kowalewski M, Kelley PH, eds. 2002. *The Fossil Record of Predation*. Paleontol. Soc. Spec. Pap. Vol. 8. New Haven, CT: Yale Univ. Repogr. Imaging Serv.
- LaBarbera M. 1981. The ecology of Mesozoic *Gryphaea*, *Exogyra*, and *Ilymatogyra* (Bivalvia: Mollusca) in a modern ocean. *Paleobiology* 7:510–26
- Laflamme M, Xiao S, Kowalewski M. 2009. Osmotrophy in modular Ediacara organisms. *Proc. Natl. Acad. Sci. USA* 106:14438–43
- Leighton LR. 2001. New example of Devonian predatory boreholes and the influence of brachiopod spines on predator success. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 165:53–69
- Leighton LR. 2003. Predation on brachiopods. See Kelley et al. 2003, pp. 215–37
- Levinton JS, Bambach RK. 1975. A comparative study of Silurian and recent deposit-feeding bivalve communities. *Paleobiology* 1:97–124
- Liu AG, McIlroy D, Brasier MD. 2010. First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland. *Geology* 38:123–26
- Lockwood R. 2004. The K/T event and infaunality: morphological and ecological patterns of extinction and recovery in veneroid bivalves. *Paleobiology* 30:507–21
- Love GD, Grosjean E, Stalvies C, Fike DA, Grotzinger JP. 2009. Fossil steroids record the appearance of Demospongiae during the Cryogenian period. *Nature* 457:718–21
- Low S. 2004. Dynamics of morphological evolution in the Nautiloidea: a computational geometric approach. *Geol. Soc. Am. Abstr. Prog.* 36:315
- Madin JS, Alroy J, Aberhan M, Fürsich FT, Kiessling W, et al. 2006a. Response to comments on “Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates.” *Science* 314:925f
- Madin JS, Alroy J, Aberhan M, Fürsich FT, Kiessling W, et al. 2006b. Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates. *Science* 312:897–900
- Marshall CR. 2006. Explaining the Cambrian “explosion” of animals. *Annu. Rev. Earth Planet. Sci.* 34:355–84
- Martin RE. 1996. Secular increase in nutrient levels through the Phanerozoic: implications for productivity, biomass, and diversity of the marine biosphere. *Palaiois* 11:209–19
- Martin RE. 2003. The fossil record of biodiversity: nutrients, productivity, habitat area and differential preservation. *Lethaia* 36:179–93

- Marx FG, Uhen MD. 2010. Climate, critters, and cetaceans: Cenozoic drivers of the evolution of modern whales. *Science* 327:993–96
- McGhee GR Jr. 1996. *The Late Devonian Mass Extinction: The Frasnian-Famennian Crisis*. New York: Columbia Univ. Press
- McGhee GR Jr, Sheehan PM, Bottjer DJ, Droser ML. 2004. Ecological ranking of Phanerozoic biodiversity crises: ecological and taxonomic severities are decoupled. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 211:289–97
- McShea DW. 1994. Mechanisms of large-scale evolutionary trends. *Evolution* 48:1747–63
- McShea DW. 1996. Metazoan complexity and evolution: Is there a trend? *Evolution* 50:477–92
- Meyer DL, Macurda DB Jr. 1977. Adaptive radiation of the comatulid crinoids. *Paleobiology* 3:74–82
- Narbonne GM. 2005. The Ediacara biota: Neoproterozoic origin of animals and their ecosystems. *Annu. Rev. Earth Planet. Sci.* 33:421–42
- Niklas KJ. 1994. Morphological evolution through complex domains of fitness. *Proc. Natl. Acad. Sci. USA* 91:6772–79
- Novack-Gottshall PM. 2007. Using a theoretical ecospace to quantify the ecological diversity of Paleozoic and modern marine biotas. *Paleobiology* 33:273–94**
- Novack-Gottshall PM. 2008a. Ecosystem-wide body-size trends in Cambrian-Devonian marine invertebrate lineages. *Paleobiology* 34:210–28
- Novack-Gottshall PM. 2008b. Using simple body size metrics to estimate fossil body volume: empirical validation using diverse Paleozoic invertebrates. *Palaïos* 23:163–73
- Oji T. 1996. Is predation intensity reduced with increasing depth? Evidence from the West Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic marine revolution. *Paleobiology* 22:339–51
- Oji T, Ogaya C, Sato T. 2003. Increase of shell-crushing predation recorded in fossil shell fragmentation. *Paleobiology* 29:520–26
- Payne JL, Finnegan S. 2006. Controls on marine animal biomass through geological time. *Geobiology* 4:1–10
- Payne JL, Finnegan S. 2007. The effect of geographic range on extinction risk during background and mass extinction. *Proc. Natl. Acad. Sci. USA* 104:10506–11
- Payne JL, Lehrmann DJ, Wei J, Knoll AH. 2006. The pattern and timing of biotic recovery from the end-Permian extinction on the Great Bank of Guizhou, Guizhou Province, China. *Palaïos* 21:63–85
- Plotnick RE, Baumiller TK. 2000. Invention by evolution: functional analysis in paleobiology. *Paleobiology* 26(Suppl. 4):305–23
- Powell MG, Kowalewski M. 2002. Increase in evenness and sampled alpha diversity through the Phanerozoic: comparison of early Paleozoic and Cenozoic marine fossil assemblages. *Geology* 30:331–34
- Pruss SB, Corsetti FA, Bottjer DJ. 2005. The unusual sedimentary rock record of the Early Triassic: a case study from the southwestern United States. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 222:33–52
- Pruss SB, Finnegan S, Fischer WW, Knoll AH. 2010. Carbonates in skeleton-poor seas: new insights from Cambrian and Ordovician strata of *Laurentia*. *Palaïos* 25:73–84
- Raup DM, Sepkoski JJ Jr. 1982. Mass extinctions in the marine fossil record. *Science* 215:1501–3
- Roopnarine PR, Angielczyk KD, Hertog R. 2006. Comment on “Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates.” *Science* 314:925d
- Sallan LC, Coates MI. 2010. End-Devonian extinction and a bottleneck in the early evolution of modern jawed vertebrates. *Proc. Natl. Acad. Sci. USA* 107:10131–35
- Schweitzer CE, Feldmann RM. 2010. The Decapoda (Crustacea) as predators on Mollusca through geologic time. *Palaïos* 25:167–82
- Seilacher A, Pflüger F. 1994. From biotopes to benthic agriculture: a biohistoric revolution. In *Biostabilization of Sediments*, ed. WE Krumbein, DM Paterson, LJ Stal, pp. 97–105. Oldenburg, Ger.: Bibl. Informationssyst. Univ. Oldenbg.

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- Sepkoski JJ Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7:36–53
- Sepkoski JJ Jr. 1982. Flat-pebble conglomerates, storm deposits, and the Cambrian bottom fauna. In *Cyclic and Event Stratification*, ed. G Einsele, A Seilacher, pp. 371–85. Berlin: Springer-Verlag
- Sepkoski JJ Jr. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10:246–67
- Sepkoski JJ Jr. 2002. A compendium of fossil marine animal genera. *Bull. Am. Paleontol.* 363:1–560**
- Sepkoski JJ Jr, Bambach RK, Droser ML. 1991. Secular changes in Phanerozoic event bedding and the biological overprint. In *Cycles and Events in Stratigraphy*, ed. G Einsele, W Ricken, A Seilacher, pp. 298–312. Berlin: Springer-Verlag
- Sheehan PM. 2001. The Late Ordovician mass extinction. *Annu. Rev. Earth Planet. Sci.* 29:331–64
- Signor PW III, Brett CE. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology* 10:229–45
- Stanley SM. 1968. Post-Paleozoic adaptive radiation of infaunal bivalve molluscs: a consequence of mantle fusion and siphon formation. *J. Paleontol.* 42:214–29
- Stanley SM. 1970. *Relation of Shell Form to Life Habits of the Bivalvia (Mollusca)*. Geol. Soc. Mem. 125. Boulder, CO: Geol. Soc. Am. 296 pp.**
- Stanley SM. 1973. An ecological theory for the sudden origin of multicellular life in the late Precambrian. *Proc. Natl. Acad. Sci. USA* 70:1486–89
- Stanley SM. 1974. What has happened to the articulate brachiopods? *Geol. Soc. Am. Abstr. Prog.* 6:966–67
- Stanley SM. 2006. Influence of seawater chemistry on biomineralization throughout Phanerozoic time: paleontological and experimental evidence. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 232:214–36
- Stanley SM. 2007. An analysis of the history of marine animal diversity. *Paleobiology* 33(Suppl. 4):1–55
- Stanley SM. 2008. Predation defeats competition on the seafloor. *Paleobiology* 34:1–21
- Steneck RS. 1983. Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* 9:44–61
- Thayer CW. 1979. Biological bulldozers and the evolution of marine benthic communities. *Science* 203:458–61**
- Thayer CW. 1983. Sediment-mediated biological disturbance and the evolution of the marine benthos. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. MJS Tevesz, PL McCall, pp. 479–625. New York: Plenum**
- Twitchett RJ. 1999. Palaeoenvironments and faunal recovery after the end-Permian mass extinction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 154:27–37
- Vermeij GJ. 1977. The Mesozoic marine revolution: evidence from snails, predators, and grazers. *Paleobiology* 3:245–58
- Vermeij GJ. 1987. *Evolution and Escalation: An Ecological History of Life*. Princeton, NJ: Princeton Univ. Press**
- Vermeij GJ. 1990. The origin of skeletons. *Palaios* 4:585–89
- Vermeij GJ. 1995. Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology* 21:125–52
- Vermeij GJ. 1999. Inequality and the directionality of history. *Am. Nat.* 153:243–53
- Vermeij GJ. 2008. Escalation and its role in Jurassic biotic history. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 263:3–8
- Wagner PJ, Kosnik MA, Lidgard S. 2006. Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems. *Science* 314:1289–92
- Walker SE, Brett CE. 2002. Post-Paleozoic patterns in marine predation: Was there a Mesozoic and Cenozoic marine predatory revolution? See Kowalewski & Kelley 2002, pp. 119–93
- Wang SC, Bush AM. 2008. Adjusting global extinction rates to account for taxonomic susceptibility. *Paleobiology* 34:434–55
- Westrop SR, Adrain JM. 1998. Trilobite alpha diversity and the reorganization of Ordovician benthic marine communities. *Paleobiology* 24:1–16
- Woodin SA, Wetthey DS, Volkenborn N. 2010. Infaunal hydraulic ecosystem engineers: cast of characters and impacts. *Integr. Comp. Biol.* 50:176–87

Xiao S, Laflamme M. 2009. On the eve of animal radiation: phylogeny, ecology and evolution of the Ediacara biota. *Trends Ecol. Evol.* 24:31–40

Yuan X, Xiao S, Parsley RL, Zhou C, Chen Z, Hu J. 2002. Towering sponges in an Early Cambrian lagerstätte: disparity between nonbilaterian and bilaterian epifaunal tierers at the Neoproterozoic-Cambrian transition. *Geology* 30:363–66

Zhuravlev AY, Riding R, eds. 2001. *The Ecology of the Cambrian Radiation*. New York: Columbia Univ. Press

A concise description of
the Ediacaran fauna.
