

## 3.3 Preservation in Different Ecological Settings

### 3.3.1 Major Biases in the Fossil Record

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#### Introduction

Palaeontologists investigate many different kinds of biological phenomena, ranging from the biomechanics of skeletal elements to the timing of mass extinctions, and so are concerned with the potential for taphonomic bias at many different scales (Table 3.3.1.1). The anatomical completeness of fossil preservation is of particular concern in studies of systematics and functional morphology; spatial fidelity (see Section 3.2.6), time-averaging (see Section 3.2.7), and ecological fidelity of fossil assemblages become significant in high-resolution evolutionary studies, palaeoecology, and biogeography; and the quality of time-series data and stratigraphic biases become especially significant in biostratigraphy, phylogeny, macroevolution, and evolutionary palaeoecology. Biochemical fidelity in investigations of isotopic and molecular palaeontology (e.g. studies of fossil diet, climate, DNA, biomarkers) could be added at the fine end of this spectrum. Any given fossil record (i.e. set of specimens, series of assemblages) thus has many different taphonomic qualities, of which only a subset may be relevant to the palaeobiological question at hand.

Although the quantification of bias is still very much at the frontier, both actualistic and stratigraphic studies indicate that most types of bias are the products of multiple intrinsic and extrinsic factors, whose rates and selectivities of damage are increasingly well known. Major sources of bias include: (1) the differing durabilities of biological materials (is the organism composed exclusively of highly volatile organic compounds or does it contain refractory organics and biominerals?); (2) the environment of accumulation (including the community of organisms that modify or destroy tissues after death, as well as the biogeochemistry of porewaters and the short-term dynamics of burial/exhumation); and (3) the postdepositional history of entombing sediments, which determines the ultimate fabric of the stratigraphic record. The challenge is to move from an appreciation of damage (i.e. states of fossil preservation, their origins, and the relative degrees of postmortem modification that they signify) to a quantitative assessment of bias (loss and other significant skewing of biological information). Biases clearly vary widely among major taxonomic groups, and probably across climatic/latitudinal and tectonic settings. The qualities of the fossil record may also have changed over geological time, a consequence of biological evolution (in both potential fossils and in tissue-destroying organisms), geological evolution of the Earth's surface (chemical changes in oceans and atmosphere, sea-level and climatic effects of plate tectonics, including latitudinal drift), and the cumulative effects of age (volume of available rock, cycles of diagenesis and tectonism).

Table 3.3.1.1 Qualities of the fossil record and sources of bias. (Adapted from Kidwell and Brenchley 1996.)

Aspect of quality	Sources of bias
Biochemical fidelity	Destruction, overprinting, and shifting of chemical compositions by diagenesis and metamorphism
Anatomical completeness	Destruction or incomplete mineral replacement of soft tissues; disarticulation, fragmentation, recrystallization, and deformation of mineralized skeletons
Spatial fidelity	Transport out of life position, life habitat, or biogeographical province
Temporal resolution	Mixing (time-averaging) of non-contemporaneous remains within the sedimentary column via physical or biological processes
Ecological fidelity	Selective destruction of species, morphs, and age classes, affecting presence-absence and relative abundance in fossil assemblages; bias from exotics and non-contemporaneous remains
Completeness of time series	Erosion or non-deposition of sediments, and taphonomic or diagenetic obliteration of fossils in surviving facies, creating gaps in the record
Stratigraphic bias	Non-random patterns both in the composition of facies because of cycles and secular trends in Earth's palaeogeography, and in the preservation of facies because their records are thin, localized, or readily eroded, preventing uniform sampling

### Biases linked to inherent differences in biological materials

Perhaps the greatest bias in the fossil record is the divide between the poor to non-existent fossil record for organisms lacking mineralized or otherwise refractory skeletons, and the good to excellent record of organisms having such hard parts. Among living intertidal macrobenthos in Washington State, USA, for example, 100% of species with sturdy calcareous shells are from genera known to have a fossil record (shelled molluscs, barnacles, tube-secreting polychaetes, irregular echinoids), 73% of species with fragile skeletons or small isolated hard parts have a fossil record (e.g. arthropods, regular echinoids, asteroids, ophiuroids, holothuroids, sponges, tunicates, some nudibranchs and polychaetes), but none of the species lacking megascopic hard parts have a record (most polychaetes, nemerteans, ascidians, hydroids, anemones, sipunculans, flatworms, jellyfish, some nudibranchs, constituting 30% of the total fauna; Schopf 1978). These figures are typical for shallow-marine macrobenthic communities (reviewed by Kidwell and Bosence 1991), and analogous effects are known or expected among other groups, for example between agglutinated and mineral-secreting foraminiferans, mineralized and non-mineralized bryozoans, soft and stony corals, woody and non-woody plants, heavily and lightly sclerotized insects (reviewed by Kidwell and Flessa 1996). Taxonomically identifiable remains of organisms lacking megascopic hard parts (Schopf's 1978 last category)—and the preservation of soft tissues in general—require unusual environmental conditions that are geologically quite rare (see Sections 3.2.1 and 3.4). Such preservation has many positive consequences—high anatomical completeness, high temporal resolution (usually an instantaneous snapshot), high ecological fidelity—but biochemical fidelity may be low (tissues are generally preserved as mineral replacements or films, not as unaltered organic compounds) and stratigraphic horizons with comparable preservation may be so widely spaced that time series are weak.

Basic differences in body composition, linked strongly with phylogeny, thus have direct and fundamental effects on the qualities of the fossil record. The magnitude of the effect on time-averaging (time interval over which a fossil assemblage accumulated; see Section 3.2.7) and species richness in assemblages, for example, can be considerable. Quantitative information remains sparse but absolute scales of time-averaging in oxygenated environments range from ecologically instantaneous ('gelatinous' organisms which will be fossilized only under catastrophic burial or exposure limited to just a few days; flowers and lightly mineralized arthropods having maximum durabilities of weeks to months in

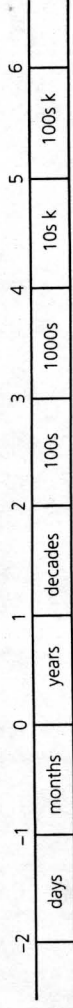
sedimentary mixing zones) to ecologically prolonged (durable hard parts of land vertebrates and marine molluscs which can survive thousands to tens of thousands of years of attritional accumulation; Fig. 3.3.1.1).

The reworking of biological remains inherent to time-averaging has disparate effects on ecological fidelity: time-averaging tends to increase the species richness of taphonomically durable groups above standing diversities (by a factor of two or three among molluscs), mixing species from different generations or even community states, but reduces the diversity of fragile groups relative to the source community (by 25% or more; Kidwell and Flessa 1996). Some interesting concordances in durability and time-averaging occur across major taxonomic divides, for example between molluscs and non-agglutinating benthic foraminiferans, notwithstanding great differences in body size and skeletal microstructure. However, 'disharmonious' time-averaging is probably common in many taxonomically diverse assemblages, even if only hard part-producing groups are considered. The organic-rich shells of lingulid brachiopods, for example, can survive only a few days or weeks of reworking in intertidal sediments, and yet co-occur with very durable mollusc shells representing centuries to thousands of years of accumulation (see references in Section 3.2.7).

Even among groups with relatively high preservation potential, a proportion of taxa will be unrecorded or severely under-represented; quantifying this bias remains an important direction of taphonomic research (reviewed by Kidwell and Flessa 1996). The major factors in differential preservation of mineralized taxa are: (1) mineral content (from a few per cent to ~99% dry weight within mineralized body parts); (2) mineral composition (aragonitic and calcitic forms of calcium carbonate, silica, and various organo-mineral forms of calcium phosphate are most common, e.g. 82% of bivalve genera with shells composed entirely of aragonite have a fossil record vs. 94% of genera with shells composed at least in part of calcite; Harper *in* Donovan and Paul 1998); (3) microstructure (variation in mineral crystallite surface area, percentage of organic matrix in the shell); (4) hard part size, shape, and density (intraskelatal porosity and growth form affect postmortem persistence and transport of bones, corals, and crinoids; size has a strong effect on pollen transport; Greenstein *et al. in* Donovan and Paul 1998; see Section 3.3.3); (5) tightness of skeletal articulation (e.g. differences among sea urchin families in anatomical completeness and in time-series data; Greenstein 1993); (6) body size (species representation in vertebrate death assemblages and age-class representation in mollusc assemblages); and (7) life habit (e.g. effects of epifaunal vs. infaunal life habit on preservation in life position among marine benthos).

Species that are rare in live communities (sparse or

YEARS OF TIME-AVERAGING PER ASSEMBLAGE (LOG SCALE)



MACROFLORA  
Recent

fresh leaves, flowers \_\_\_\_\_  
cuticle, leaf fall \_\_\_\_\_  
cones, seeds, bark \_\_\_\_\_ peat \_\_\_\_\_

Cretaceous-Palaeogene

plant bed \_\_\_\_\_  
florule \_\_\_\_\_  
megafossil flora \_\_\_\_\_  
biostratigraphic zone \_\_\_\_\_

POLLEN  
Quaternary

lake lamina \_\_\_\_\_  
1-cm core top \_\_\_\_\_  
regional pollen map \_\_\_\_\_

VERTEBRATES  
Quaternary

temperate/tropical Arctic land surfaces \_\_\_\_\_  
downward intrusion \_\_\_\_\_ cave sites \_\_\_\_\_  
fluvial reworking \_\_\_\_\_  
bioturbation \_\_\_\_\_  
sediment flow and cryoturbation \_\_\_\_\_

Cretaceous

nests and event beds \_\_\_\_\_  
attritional microsites \_\_\_\_\_  
channel lags \_\_\_\_\_

Actualistic simulation

attritional land surface \_\_\_\_\_

TERRESTRIAL SYSTEMS

MACROINVERTEBRATES  
Recent

intertidal and nearshore \_\_\_\_\_  
shelf \_\_\_\_\_

Post-Palaeozoic

event concentrations of within-habitat time-averaged shells \_\_\_\_\_

censuses \_\_\_\_\_

composite concentrations of within-habitat time-averaged shells \_\_\_\_\_

hiatal concentrations of within-habitat time-averaged, environmentally condensed, and biostratigraphically condensed shells \_\_\_\_\_

Palaeozoic

single event beds \_\_\_\_\_

composite fossil beds \_\_\_\_\_

hiatal fossil beds \_\_\_\_\_  
lag accumulations \_\_\_\_\_

BENTHIC FORAMINIFERA  
Recent

shell-poor siliciclastic shelf \_\_\_\_\_

carbonate and shell-rich siliciclastic shelf \_\_\_\_\_  
dissolution-dominated abyss \_\_\_\_\_  
reworking-dominated abyss \_\_\_\_\_  
condensed biozones \_\_\_\_\_

GENERAL SIMULATIONS  
Based on sedimentation rates

shallow marine shelf and platform \_\_\_\_\_  
continental rise \_\_\_\_\_

alluvium \_\_\_\_\_  
alluvium \_\_\_\_\_

Mean residence time in benthic mixed layer =

shelf/platform \_\_\_\_\_  
continental rise \_\_\_\_\_  
abyss \_\_\_\_\_

Fig. 3.3.1.1 Absolute durations of time-averaging. Estimates are based on diverse types of data, including extrapolations from modern rates of decay and disintegration, direct dating of specimens in modern death assemblages, inferred

accumulation history of fossil concentrations, stratigraphic context, and probabilistic analysis of sedimentation rates. (Adapted from Kidwell and Behrensmeier 1993.)

MARINE SYSTEMS

patchy distributions) also have low probabilities of being known from the fossil record. Because sampling is never complete, datasets are biased against rare species, so much so that some authors suggest ignoring them entirely (but see Culver and Buzas *in* Donovan and Paul 1998). However, relatively high ecological fidelity is indicated if species that are rare when alive are also rare in death and fossil assemblages. Living communities and local death assemblages show high statistical agreement in species rank-order for many groups (molluscs, land mammals, pollen, leaves; reviewed by Kidwell and Flessa 1996). Crabs and echinoids show poor live/dead agreements, and corals yield mixed results (good agreement between live communities and local Pleistocene fossil assemblages, but poor agreement between live and locally accumulating dead debris; Greenstein *et al.* *in* Donovan and Paul 1998).

### Biases linked to postmortem environment

The major environmental divide in the quality of the fossil record is between land, which is dominated by erosion and weathering, and seas, which are overall sinks for sediment and are commonly oxygen-limited, especially in early diagenetic porewaters. Most palaeontologists would agree that land fossils are far less abundant and more patchy in distribution than marine fossils, even if microfossils are excluded (e.g. Benton and Simms 1995), but separating the effects of taphonomic environment from taxonomic composition is difficult. For example, is the fossil record of marine vertebrates (or arthropods or molluscs) more complete than the record of their terrestrial relatives? It probably is, but both realms are mosaics of physical and chemical conditions and, viewed globally, exhibit a comparable spectrum of fossil preservation, ranging from spectacular soft-tissue Lagerstätten to lags of only marginally identifiable skeletal debris. Consequently, differences in taphonomic bias across this environmental divide are probably more in degree than in kind.

A wide array of environmental agents and circumstances, acting alone or in combination, determine preservation in the very early phases of fossilization, and actualistic information on these factors drive expectations of bias in the fossil record. *Biological factors* in tissue preservation include the activities of predators and scavengers (which may destroy mineralized hard parts and/or transport remains out of the life habitat), bioturbators (which aerate and acidify porewaters, and also advect tissues), bioeroders/macerators, and encrusters (including microbial precipitation of minerals). *Physical factors* include timing of burial after death, sediment winnowing and physical reworking of specimens with or without out-of-habitat transport (see Section 3.2.6), net sediment accumulation rates (affecting average transit time to permanent burial level), light (UV

weathering of bones; activity of photosynthetic bioeroders/encrusters), seasonality (pulsed vs. continuous carcass production), and specialized physical conditions of soft-tissue conservation (ice, desiccation). *Chemical factors* include oxygen levels (which drive hydrolysis and aerobic decomposers; anoxia excludes metazoan predators, scavengers, and bioturbators), mineral saturation state of water, acidity (antibacterial), sediment composition (availability of organic matter, iron and other metals for anaerobic decomposition pathways, silica for silicification, clays for organic adsorption), and nutrient levels (affecting organic production rates, intensities of bioerosion/encrustation; see Sections 3.2.2 and 4.2.8).

Most information on environmental trends in bias comes from studies in temperate latitudes. Marine basins show no simple monotonic trends in anatomical completeness and time-averaging with water depth or distance offshore (Fig. 3.3.1.2) because of the geomorphic complexity of coastal regions and the opposing trends of water energy (generally higher onshore) and net sediment accumulation rates (generally decreasing offshore in both siliclastic and carbonate systems, but with onshore areas of erosion, bypass, and exposure). High-fidelity snapshot-type preservation is most common in lagoons and in offshore transition zones of maximum poststorm deposition. Relatively low-resolution environmentally condensed assemblages are most common in nearshore areas where facies shift rapidly, and net rates of sediment accumulation can be locally low. The ecological and spatial fidelity of molluscan death assemblages to local live communities is comparably high in level-bottom environments. These qualities of death assemblages do not appear to vary dramatically among freshwater, intertidal, coastal subtidal, and open shelf settings in temperate latitudes (reviewed by Kidwell and Flessa 1996), but the extent of latitudinal variation is still unknown.

In non-marine deposits, scales of time-averaging also vary dramatically among subenvironments (reviewed by Kidwell and Flessa 1996). Lakes provide both 'snapshot' censuses and time-averaged assemblages with decadal resolution (pollen, fish, insects, leaves, including some of the highest anatomical resolution of soft tissues); channel-fills and floodplain ponds typically yield time-averaged assemblages reflecting years to hundreds of years of skeletal accumulation; and most channel lags and palaeosols permit only hundreds to thousands of years' time resolution (Fig. 3.3.1.1). Spatial and ecological fidelity (presence-absence and rank order of species) are high for land mammals in the few environments tested, although differences in relative abundances in the living community are magnified in death assemblages. Spatial fidelity is high for pollen in all environments if only small-area lakes and other traps are sampled, and ecological fidelity is high if only wind-

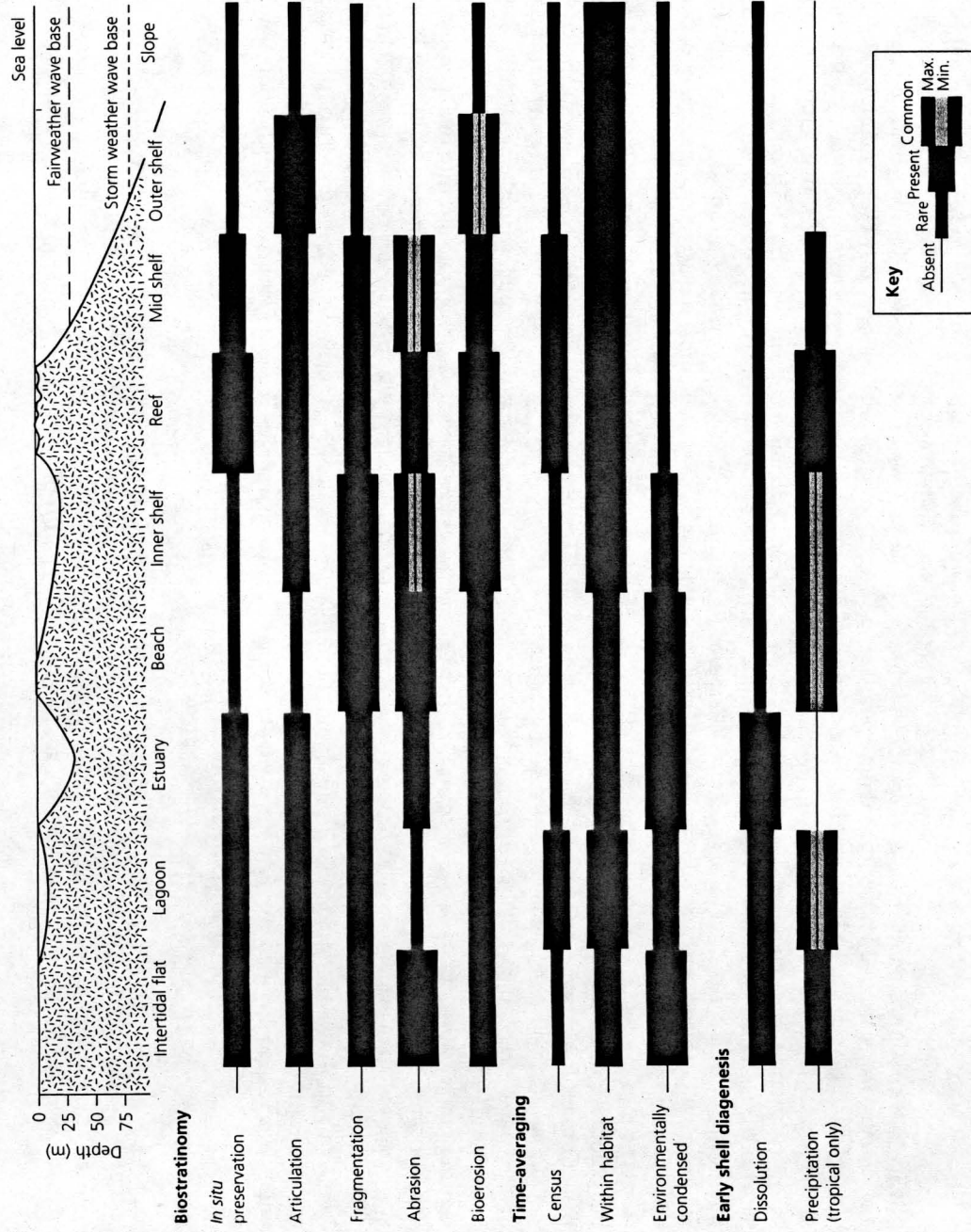


Fig. 3.3.1.2 Summary trends in types of damage and in bias for molluscan hard parts in marine environments. *In situ* preservation (in life position) and articulation signify high

anatomical completeness. For absolute durations of time-averaging levels, see Fig. 3.3.1.1. (From Kidwell and Bosenne 1991.)

pollinated plants are considered. Both qualities are high for leaf litter on temperate forest floors, but ecological fidelity is low for litter in tropical forests owing to their greater heterogeneity. Data on possible climatic trends in bias are sparse for other groups, but there appears to be lower spatial resolution in high-latitude insect assemblages than in low latitudes (Ponel and Richoux 1998), and greater durability and thus more time-averaging of land mammal bones in the Arctic than in temperate and tropical settings (Graham *in* Kidwell and Behrensmeyer 1993).

The potential biases imposed by environmental gradients can be avoided or minimized if care is taken to include only 'isotaphonomic' assemblages, i.e. fossil assemblages having taphonomically comparable histories of accumulation as judged from the state of preservation of surviving material and the sedimentological context.

### Biases linked to sedimentary history and basin type

The ultimate filter on the quality of a particular fossil record is the fate of entombing sediments: diagenesis and erosion that locally degrade or obliterate the fossil record will limit both palaeogeographical (time-slice) and time-series information. Such destruction is not randomly distributed, but tends to be focused on the records of particular environments, sea-level phases, and tectonic settings/conditions. Palaeontologists have begun to evaluate the taphonomic consequences of this in a sequence-stratigraphic context at both basin and global scales (Brett 1995; see Section 5.4.5). Within marine siliclastic sequences, for example, transgressive tracts are commonly thinner and have greater potential for skeletal lags and environmental condensation of faunas; assemblages from regressive/progradational

phases tend to have higher time resolution and simpler histories of accumulation but are more likely to be affected by meteoric diagenesis and erosional removal; and sequence-bounding unconformities and other hiatuses are less severe and more localized in rapidly subsiding tectonic basins, so that time-averaging and taphonomic complexity of skeletal concentrations are lower than in other settings (Kidwell *in* Kidwell and Behrensmeier 1993). Analogous stratigraphic bias is observed in non-marine vertebrate records. For example, low subsidence rates that favour prolonged fluvial reworking and close-stacking of channels reduce the preservation potential of snapshot assemblages, as observed both through base-level cycles and across fore-land basin gradients in stratigraphic accommodation (e.g. Rogers *in* Kidwell and Behrensmeier 1993 and references therein).

Hiatuses and extreme slow-downs in sedimentation, and diagenetic removal of fossils, make species ranges shorter and more discontinuous, a phenomenon evident at both sequence and larger scales (e.g. Paul and Donovan *in* Donovan and Paul 1998). In some instances, gradual trends may be made to appear sudden (e.g. erosional truncation causing last appearances to coincide at a single stratigraphic horizon), whereas in other instances coincidental events may be smeared into a gradual pattern (e.g. progressive change in facies, causing some species to disappear prematurely from a local record for ecological or taphonomic reasons). Because increased sampling cannot always compensate for such gaps, various methods have been developed to estimate the magnitude of the effect. These include the calculation of confidence limits for range end-points (based on gaps between occurrences within the known range, either biostratigraphic or biogeographical; Marshall *in* Donovan and Paul 1998), taphonomic control taxa (absence of a taxon is not a preservational artefact if another taxon with similar ecology and preservation potential is present, e.g. cyclostome bryozoans as control taxa for cheilostomes; Boffter and Jablonski 1988), and 'Lazarus taxa' (the percentage of taxa that appear to become extinct, but then reappear later in the stratigraphic record, gives a measure of quality of time-series data for that interval; Jablonski 1986; see Sections 5.4.3 and 5.4.5).

There are also non-random patterns in the creation of environmental conditions favourable to fossilization, so that upland ponds/lakes, estuaries (flooding incised river valleys to make excellent vertebrate traps), anoxic lagoons (e.g. many Jurassic soft-tissue Lagerstätten), and authigenic phosphate and glauconite beds are most common during transgression. The high abundances of marine soft-tissue Lagerstätten during the Cambrian and Jurassic (Allison and Briggs 1993a), which are both transgressive phases of first-order sea-level cycles, perhaps reflect such geological control. Such geological

factors create a fundamental fabric of facies types and gaps in the stratigraphic record, within which palaeontological collecting and analysis are constrained.

### Megabiases — secular trends in qualities of the fossil record

There are many reasons to suspect that the quality of the fossil record may vary significantly with altitude/latitude/climate and over evolutionary time, due to differences in organisms and in geological conditions, but there are few empirical data relevant to these issues. This is of particular concern because of strong collecting bias by palaeontologists toward North America and Europe: both continents have drifted extensively through the Phanerozoic, so that their shallow seas were largely tropical during the Palaeozoic and non-tropical in later times. Collection bias has thus perhaps underestimated species richness per myr of the Permian by more than 100%, making it the most diverse period of the Palaeozoic, and underestimated post-Palaeozoic species richnesses by  $\approx 50\%$ , assuming that past latitudinal diversity gradients were as steep as in the Recent (Allison and Briggs 1993b). Other sampling factors with potential to bias large-scale palaeobiological patterns such as Phanerozoic diversity trends include the decline in outcrop area or rock volume with increasing geological age, and differences in monograph effort among geological periods and taxonomic groups (e.g. Sepkoski *et al.* 1981).

Geological factors are extremely important in patterning the record on time scales up to  $\approx 50$  myr (second-order stratigraphic sequences; see above). Longer-scale trends, however, appear to be driven primarily by changes in ocean/atmospheric chemistry and by evolution in biological processes, including both the production and the destruction/recycling of organic compounds and biominerals. Some of the most striking changes in styles of soft-tissue preservation occur in the late Precambrian–Cambrian interval. The advent of metazoan scavenging of collagen, the intensification of bioturbation, and physicochemical oceanographic changes in clay minerals have been variously invoked to explain the abrupt termination of the Ediacaran faunal record (sandstone impressions) and the exclusively Late Riphean to Middle Cambrian window of Burgess Shale-type preservation, in which non-mineralizing taxa are known from carbonaceous compressions (Jensen *et al.* 1998; Orr *et al.* 1998). In the Phanerozoic, changes in skeletal microstructure and ocean chemistry have been invoked to explain cyclic and secular changes in the quality of the marine microfossil record (Martin 1995). A proportional shift from calcite to aragonite precipitation among macrobenthos and a decline and retreat offshore of siliceous sponges may be responsible for a secular

decline in silicified shallow marine faunas, with implications for quality of skeletal preservation, intensity of palaeontological study, and numbers of Lazarus taxa (Schubert *et al.* 1997). An increase in the maximum thickness of dense-packed skeletal concentrations of benthic macrobenthos from the early Palaeozoic to the Neogene has been interpreted in terms of an increase in shell durability, the invasion by shell-producers of high-energy environments where postmortem winnowing is more common, and, perhaps, an increase in rates of shell production (Kidwell and Brenchley 1996). Evolutionary changes among shell-destroyers and purely geological factors evidently played a lesser role. The most likely effect on bias is an increase in time-averaging per assemblage over time and, perhaps in hand with this, a reduction in ecological fidelity: hand samples will capture different amounts of time depending on their geological ages. Taphonomic qualities of other records may also have changed in response to evolution of hard part producers, for example the land vertebrate record (e.g. dry land was not fully exploited until the late Palaeozoic, and mammal bones are generally more porous than reptile bones). However, net effects and specific drivers are difficult to predict given the many conflicting factors (e.g. changes in styles and metabolic rates of bone-crushing predators, no clear body size trends in prey, strong period-to-period bias in range of continental latitudes and aridity), and thus the determination of secular trends will almost certainly require an empirical survey of the fossil record itself.

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## 3.3.2 Benthic Marine Communities

W.D. ALLMON

### Introduction

In diversity of taxa and abundance of individuals, benthic marine invertebrates constitute the majority of the fossil record. Although it is likely that the fossil record of benthic marine organisms is among the most complete of all major environmental settings, not all benthic marine invertebrate species in a community are equally likely to be fossilized, and their relative abundances or ecological relationships may not be preserved. Analysis of the likelihood of preservation of particular taxa, and of benthic marine communities in general, has important implications for understanding patterns of evolution of individual organisms and communities, as well as larger patterns of diversity and

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To the memory of J.J. Sepkoski Jr

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