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Seafood through time: changes in biomass, energetics, and productivity in the marine ecosystem

Richard K. Bambach

Abstract.—The biomass of marine consumers increased during the Phanerozoic. This is indicated by the increase in both fleshiness and average size of individuals of dominant organisms, coupled with the conservative estimate that dominant organisms in the Cenozoic are at least as abundant as those in the Paleozoic. As faunal dominants replaced one another during the Phanerozoic the general level of metabolic activity increased due to both increase in basal metabolism and increase in more energetic modes of life. This demonstrates that the expenditure of energy by marine consumers has increased with time as well. There is a time lag in the expansion of more energetic life habits from environmental settings known to have high food supply into regions expected to have lower rates of food supply (e.g., bivalves into offshore carbonate environments or deep burrowing deposit feeders into the full range of shelf environments), and a time lag in diversification of energetic modes of life (e.g., predation or deep burrowing deposit feeding) for long intervals after they first appeared. This suggests that the supply of food increased across the whole spectrum of marine habitats during the Phanerozoic. The great diversification of specialized predators especially suggests that biomass increase took place all the way down the food chain to the level of primary production. The development of plant life on land and the impact of land vegetation on stimulating productivity in coastal marine settings, coupled with the transfer of organic material and nutrients from coastal regions to the open ocean, and the increase through time in diversity and abundance of oceanic phytoplankton all point to increased productivity in the oceans through the Phanerozoic.

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Introduction

In this essay, I argue that biomass and energy flow have increased in the marine biosphere over time and that these increases are based on increased primary productivity in addition to increased effectiveness in utilizing resources. Overall trends in biomass, faunal energetics and implied productivity in the oceans are examined, but not perturbations of the ecosystem such as those that may be produced by anoxic events, mass extinctions or the influence of climate change on upwelling. While anecdotal and descriptive, the paper cites unambiguous and robust patterns. On the global scale considered here an effort at quantification would be too speculative at this time.

A variety of viewpoints have been expressed about biomass, nutrients and productivity through time. Jackson (1975) suggested that productivity had increased gradually through the Precambrian and more rapidly through the Phanerozoic whereas Van

Valen (1976) felt that "trophic energy" had been approximately constant since the middle Precambrian. Tappan (1982, 1986) argued that nutrient supply to the oceans has decreased through the Phanerozoic, forcing both productivity crises (mass extinctions) and evolutionary innovations to adapt to lower nutrient levels. Vermeij (1987, 1992) on the other hand, has argued that nutrient availability and productivity played essential roles in extrinsic control of evolutionary escalation, that the replacement of low energy groups by high energy groups during the Phanerozoic reflected, at least in part, competitive interaction and that the greatest episodes of escalation coincided with periods of increased primary productivity.

My focus in this paper is to demonstrate that a variety of observations about the fossil record are, in fact, examples of increase in biomass, energetics, and productivity. The concepts developed here are an extension of ideas about low nutrient levels in the early

Paleozoic first presented in 1973 (Calef and Bambach 1973) and further elaborated in a discussion group on energy and community evolution organized by Leigh Van Valen at the International Congress of Systematic and Evolutionary Biology in 1990 (Maiorana and Van Valen in press).

The Argument.—The argument for an increase in primary productivity and a concomitant increase in the supply of food and energy to marine consumers during the Phanerozoic is as follows:

- (1) Diversity, ecosystem complexity, and the utilization of ecospace have increased during the Phanerozoic. Even without an increase in total productivity, more resources must now be consumed in the marine ecosystem than in the past because resources from previously unexploited ecospace are now being utilized.
- (2) The total biomass of marine consumers has increased.
- (3) More energetic modes of life have become common among dominant macroscopic organisms. Active, high-metabolic-rate modes of life have replaced more passive modes in some cases. In other cases more active modes of life have been added to the ecosystem while passive modes persisted.
- (4) Within any particular Bauplan the effectiveness of nutrient acquisition does not increase with time, although increased resource partitioning (specialization) may occur if resources become more abundant. Generally, increase in effectiveness of resource utilization occurs only by the development of new major groups.
- (5) Because feeding efficiency does not increase with time within established modes of life, the long delay involved in the spread of organisms with more energetic modes of life from settings with established high rates of food supply in the early to mid-Paleozoic into habitats with lower relative rates of food supply in the Mesozoic and Cenozoic is indirect evidence of an increase in food availability in the marine ecosystem.
- (6) An increase in the biomass at the base of

the food chain (i.e., an increase in primary productivity) was necessary to support the increases in biomass, metabolic rates, tiering (both above and below the sediment/water interface), and predation that have occurred during the Phanerozoic.

- (7) Evidence of increased global productivity during the Phanerozoic comes directly from both the rise of life on land and the increase in diversity of marine phytoplankton.

Increasing Diversity, Ecologic Complexity, and Realized Ecospace

Despite the biases inherent in the geologic record and doubts about the validity of some taxa used in the analyses, there is no question that diversity in the marine realm increased during the Phanerozoic (Sepkoski et al. 1981; Signor 1990; Sepkoski 1992, 1993; Bambach and Sepkoski 1992). As diversity increased, the dominance structure of the fauna changed by adding newly diversified taxa while old persisted and by replacing formerly diverse taxa with newly diversified groups. These changes in faunal dominance extend beyond the class level, which characterizes Sepkoski's three evolutionary faunas (Sepkoski 1981), to changes within classes as well (Bambach 1985).

Major expansion in fully exploited ecospace accompanied faunal diversification and turnover (Bambach 1983, 1985). In the Cambrian the dominant organisms of the low diversity fauna (e.g., trilobites, inarticulate brachiopods) occupied a limited range of ecospace, primarily epifaunal suspension feeding and shallow infaunal deposit feeding modes of life. The more diverse fauna of the rest of the Paleozoic (dominated by articulate brachiopods, bryozoans, and a variety of other groups) packed epifaunal and shallow infaunal ecospace tightly and expanded into the pelagic realm. Deep infaunal activity and a wider range of predators began to develop in the mid-Paleozoic. During the Mesozoic and Cenozoic, the diversification of modern faunal dominants (bivalves, gastropods, malacostracans, echinoids, and teleost fish among others) resulted in full scale exploitation of deep infaunal modes of life and a vast expansion of predation, along with the contin-

ued occupation of the full range of epifaunal, shallow infaunal and pelagic modes of life.

The expansion of realized ecospace is not just a general property of the global fauna. It pervades ecosystem structure down to the community level and is reflected in the larger number of guilds (groupings of resource competitors) represented in Cenozoic fossil communities as compared to the Paleozoic (Bambach 1983). Within-habitat species richness in the Paleozoic had a median value of 20 for the shelf communities studied whereas comparable Neogene fossil communities had a median species richness of 42. The median number of guilds in the same fossil communities was 11 in the Paleozoic but rose to 18 for the Neogene. The doubling of species richness within communities was accompanied by the near doubling of the number of guilds represented. However, within-guild species richness patterns have remained similar for the past 450 m.y. Even low diversity communities (<16 species) commonly have eight to ten guilds represented and species per guild ratios of 1.3 to 1.5. Intermediate diversity communities (species richness of 20–45) have an average of two species per guild, and diverse communities (>45 species) maintain a species per guild ratio of about three up to very high diversities. This is true for the Paleozoic as well as the Cenozoic. Because guilds were defined on the basis of very general criteria for space utilization, feeding type, and Bauplan, the number of guilds recognized is not simply an artifact of the number of species (Bambach 1983). The near doubling in the number of modes of life in more diverse Cenozoic communities was not accomplished by packing most additional species into old guilds and only adding a few species in the new guilds. It was achieved by distributing most additional species among additional guilds. As general diversity increase within communities took place the utilization of ecospace within habitats expanded. The path to increased diversity has been by tapping new resources, not by finer scale resource partitioning.

The spread of life into previously unutilized ecospace (that is, the realized use of a larger proportion of potential ecospace) im-

plies that the realized nutrient and energy supply to marine consumers would have increased even if there had not been an increase in total resource supply. However, as will be shown below, the expansion of realized ecospace probably maps the greater availability of food and energy, not just the exploitation of previously underutilized resources.

Increase in Biomass

Because diversity does not necessarily equate to abundance we cannot read the known increase in the diversity of marine consumers as direct evidence of an increase in biomass. However, if we focus on the dominant (numerically abundant) megafossil taxa from different times and can demonstrate that common organisms in the Cenozoic were at least equal in abundance to those in the Paleozoic, then we can claim total biomass has increased if the average biomass per individual has increased. Evaluation of biomass per individual can be made directly from comparative anatomy but evaluation of abundance from different times is a taphonomic issue.

Evaluating Numerical Abundance

Precise numerical data from the fossil record are difficult to assess, given the variability of rates of sedimentation and the variety of mechanisms that form fossil assemblages (Kidwell 1986; Kidwell et al. 1986; Parsons and Brett 1991; Kidwell and Boscence 1991). Fortunately, one of the general principles of geology is actualism. Rates of sediment accumulation may have fluctuated widely but the same physical mechanisms have been involved at all times throughout geologic history. Therefore, if thickness and frequencies of fossil concentrations are comparable from different times we can argue that the abundance of organisms available to form these fossil concentrations must have been about the same—and if a secular change occurs in the thickness and frequency of fossil concentrations then a similar change in general abundance of potential fossils can be assumed.

Kidwell (1990) recognized two biostratigraphic modes of shell concentration, which

she documented from both the literature and her personal observation. The "archaic mode" is primarily thin bioclastic concentrations, which are common in Paleozoic and Triassic strata, while the "modern mode," common in Cretaceous and Cenozoic strata, has concentrations of variable thickness, which include common shell beds more than one meter thick. Kidwell observed that both modes occur in the Jurassic of England and are also taxonomically distinguishable, with brachiopods abundant in "archaic mode" thin concentrations and bivalve mollusks abundant in "modern mode" concentrations. Although recent taphonomic experiments show that brachiopod shells may break down more rapidly than bivalve shells (because of the decay of their higher content of organic matrix), my observations on Paleozoic shell accumulations from environments inhabited by both brachiopods and bivalves suggest that this potential taphonomic bias is not a serious issue, at least for storm-generated shell beds, a common mode of forming shell concentrations. The relatively uncorroded surfaces and commonly whole condition of the valves that make up the bulk of rapidly formed storm-generated shell beds show that most valves buried in such shell concentrations were recruited before serious degradation had begun. In Ordovician and Silurian storm-generated shell beds preferential loss of bivalves, rather than brachiopods, may occur because of complete solution of buried aragonitic bivalve shells, which could not be reworked, even though molds were visible in interbedded unworked sediments that also contained sound calcitic brachiopods (Kreisa and Bambach 1982). I have observed similar patterns in Devonian and Pennsylvanian concentrations as well.

None of the 40 "archaic mode" concentrations Kidwell studied from the Jurassic was more than 60 cm thick and only 12.5% were over 30 cm thick, whereas 22 of 134 (16.4%) "modern mode" concentrations were one to two meters thick and another 30 (22.4%) were 30 cm to 1 m thick. My own work in the Paleozoic (Ordovician: Kreisa and Bambach 1982; Springer and Bambach 1985; Silurian:

Levinton and Bambach 1975; and work in progress in the Pennsylvanian) further supports Kidwell's view of Paleozoic concentrations as characteristically thin, as do the data in Larson and Rhoads (1983). Although Kidwell notes that there are some thicker fossil concentrations in Paleozoic rocks, my observations on such concentrations in the *Orthorhynchula* Zone at the top of the Martinsburg Formation (Late Ordovician) in southwestern Virginia and from the easternmost facies in the Devonian Hamilton Group in New York reveal that (a) thick Paleozoic shell beds are much more localized and discontinuous than the thicker accumulations in the Cenozoic (Kidwell 1988, 1989), and (b) they occur predominantly in shallow near-shore environmental settings that often contain significant elements of Sepkoski's "modern fauna" (Sepkoski and Miller 1985). Most open shelf fossil concentrations through the Paleozoic and into the early Mesozoic fit Kidwell's "archaic mode." Therefore, although we can make no precise numerical evaluation, it is apparent that, because Cenozoic shell accumulations are as common as but generally thicker and more extensive than those of the Paleozoic, the number of common benthic organisms in the late Mesozoic and Cenozoic was probably considerably greater than it was throughout the Paleozoic, at least within the local habitats from which preserved fossil assemblages were derived. Certainly, despite some potential taphonomic bias, it is clear that Cenozoic benthic organisms were not less abundant than those in the Paleozoic. Conservatively, we can assume that Paleozoic and Cenozoic benthic organisms were equal in abundance.

Translating this to a global scale is more difficult because fluctuations in sea level change the area of marine habitat, especially the shelf habitats from which most marine megafossil assemblages are derived. However, the purposes of this paper are to examine overall trends, not shorter term perturbations. Sea level and shelf area, integrated over time intervals of 100–200 m.y., have probably been roughly equivalent throughout most of the Phanerozoic. The Pleistocene

low stands, the Late Cretaceous high stand, and intermediate Eocene and Miocene sea levels all occurred in the time span in which the "modern fauna" has been dominant; the Late Permian low stand, the Silurian high stand and various fluctuations in the Carboniferous all occurred during the dominance of the "Paleozoic fauna." Because of the constant geographic changes produced by the continuing process of plate tectonics, no unidirectional trend in habitat distribution or area exists for the Phanerozoic as a whole, as demonstrated in a variety of recent evaluations of the sedimentary record (Ronov et al. 1980; Gregor 1985; Tardy et al. 1989; Bluth and Kump 1991). Tardy et al. (1989: pp. 468, 477) even calculate average land area and average sedimentation rate for the Phanerozoic and show the period-by-period fluctuations around the average values, higher in some intervals, lower in others, but not trending up or down over the whole time span. Just as it is reasonable to assume, for local habitats, that Cenozoic organisms are at least as common as Paleozoic dominants were, it is reasonable, understanding that these comparisons are for the average over long time spans and not for specific short intervals, to argue that global distributions of habitats and, therefore, total abundances of organisms, were similar also.

Biomass Comparisons

General.—Some dominant groups have persisted and others have declined as the marine fauna has diversified. At the same time, other groups have risen in dominance, some being added to create increased taxonomic and ecological diversity, others replacing fading groups in similar niche space. The contrast between the common animals of the Paleozoic and those of the Cenozoic is striking. In general terms the Paleozoic dominants were low in individual biomass, their living tissue often arrayed as a thin two-dimensional film coating the skeleton, but their replacement groups in the Mesozoic and Cenozoic and those added into the ecosystem are generally high biomass organisms, often with three dimensional masses of fleshy tissue (e.g., visceral humps, muscular abdomens). Most of

the examples given here are well known, easily documented by reference to standard texts (Boardman et al. 1987; Pearse et al. 1987). The following examples are not exhaustive, only illustrative of the increased biomass of modern faunal dominants as compared to Paleozoic dominants.

Articulate Brachiopods versus Bivalve Mollusks.—Articulate brachiopods are the numerically dominant organisms in most Paleozoic fossil assemblages. Although the brachiopod shell can be globose and several centimeters in size, the living tissue in an articulate brachiopod is simply a small visceral mass in the beak area of the shell with slender diductor, adductor and adjustor muscles, a filamentous lophophore, a thin mantle covering the interior of the valves and, in some forms, a short pedicle. There is so little biomass in many brachiopods that the small volume of living tissue in punctae in the shell may comprise a significant portion of the total amount. The space enclosed by the shell is not filled with flesh, but serves as a filtration chamber in which the lophophore is displayed. In some concavo-convex forms (*Rafinesquina*, for example) the lophophore was apparently arranged in a more planar fashion and the volume for living tissue in the closed shell was less than the volume of an individual valve. In contrast, bivalve mollusks, the numerical dominants in most thick "modern mode" shell accumulations of the Cenozoic, have considerably greater individual biomass. Fleshy tissue (the foot, visceral mass, adductor muscles, and, in many infaunal forms, the siphon) nearly fills the inflated interior space between the valves of bivalve mollusks. Restaurant menus featuring mussels, oysters, clams and scallops attest to the gastronomic potential of these fleshy creatures—but recipes for articulate brachiopod chowder are unknown.

Trilobites versus Crabs and Lobsters.—Trilobites were the numerical dominants of the Cambrian fauna and remained significant members of the benthos until the Late Devonian. Anatomical studies of exceptionally preserved specimens, such as those on *Triarthrus* from the Ordovician in which the soft parts were pyritized (Cisne 1974, 1975), reveal

that the soft tissues were concentrated in the axial lobe. The gut and surrounding muscles extended straight back from the stomach located in the glabella. The pleural lobes of the skeleton were only a cover for the feathery exites and slender telopods (walking legs). Trilobites were flat, not fat, with the flesh arranged as in a worm with legs. However, crabs and lobsters, common larger benthic arthropods of the modern fauna, have extensively developed soft tissue and much higher individual biomass. The musculature of the abdomen is well developed, the legs have some volume and the musculature of the large claws and of the segments posterior to the walking legs in lobsters, is quite massive. Although some predation scars have been found on some trilobites, trilobite preservation is often remarkable for the undisturbed articulation of the multi-part skeleton. Many dead trilobites were not even scavenged. But crabmeat, soft-shell crab, crab legs, and lobster are gourmet delicacies—for octopus as well as people.

Echinoderms.—The abundant Paleozoic echinoderms were blastozoans and crinoids. Although they had calyces that enclosed the viscera, this was a rather small part of the whole organism and the rest (stalk, arms, pinules) was only coated by a thin film of living tissue. The common echinoderms of most modern faunas are the echinoids. Not only is the average volume of the echinoid test far greater than that of the average crinoid calyx, the large mass of the soft parts filling that space attracts the attention of a variety of predators as a food supply.

Persistent and Expanding Groups.—Sponges, coelenterates, bryozoans, archaeogastropods and cephalopods are examples of groups of organisms which were common in the Paleozoic and are still abundant. Some have low and some have high individual biomass. Because they are still abundant we can assume they contribute at least as much biomass to the modern fauna as they did to the Paleozoic fauna. But the caenogastropods and teleost fish underwent huge evolutionary radiations in the late Mesozoic and early Cenozoic. The new gastropod groups and the chordates are high individual biomass organisms and, as

with the increased biomass in replacement groups, the new biomass added by the diversification of these groups increased total biomass.

Worms.—Even though the taxonomic makeup of the burrowing infauna is not preserved, the soft-bodied infauna can be monitored by the degree of bioturbation preserved in sediments. As will be discussed in more detail in the section on increasing energetics in the marine biosphere, the degree of bioturbation has increased with time (Thayer 1983; Brandt 1986; Sepkoski et al. 1991), as has the diversity of trace fossils (Crimes 1974; Seilacher 1974). Neither would have been possible if the amount of soft-bodied infauna had decreased with time. The evidence, instead, points to an increase in soft-bodied infauna and a concomitant increase in the biomass it contributes to the total fauna.

Size and Biomass.—The average size of marine organisms has increased with time (as stated by Cope's Rule). This holds for both evolution within groups and for the average size of taxa that became dominant in the Mesozoic and Cenozoic compared to groups common early in the Paleozoic. All of the groups and comparisons cited above support this point. Increase in size strongly increases biomass because change in linear dimensions exponentially affects volume.

Stanley (1973) has pointed out that Cope's Rule may be an epiphenomenon, operating entirely (or predominantly) as a function of chance alone. If organisms start out small they can expand their size range in only one direction at first (to larger sizes). Later the chance of increase in size for large organisms will be the same as that of size decrease. The overall size distribution within a higher taxon may remain strongly right skewed, with few larger species, but the mean size will continuously shift to larger values as long as larger species arise. For example, the only Early Cambrian bivalves, *Fordilla* and *Pojetaia*, were tiny—both less than 2 mm in length (Pojeta 1975; Runnegar and Bentley 1983). Equally small bivalves still exist, but numerous larger forms have evolved during the last 550 m. y. (including meter length inoceramids in the Cretaceous and the giant clam *Tridacna* in

modern oceans). Thus the average size and, therefore, the average biomass of all bivalves summed together has shifted to ever larger values.

Conclusion about Biomass

Because the dominant organisms in Cenozoic and modern habitats have higher biomass per individual than Paleozoic dominants and are at least as common as the dominant organisms in the Paleozoic, the biomass of consumers within habitats has undoubtedly increased during the Phanerozoic. Because the average thickness of shell accumulations has increased with time it is probable that abundances have actually increased, making the case for an increase in biomass within habitats even stronger. Because there has not been a secular loss of habitat area over the time scale considered here, it is reasonable to conclude that total biomass has increased in the marine biosphere during the Phanerozoic.

Increase in Faunal Energetics

General Physiological Changes

Not only has the biomass of the marine biota increased, the energetics of many groups that dominate Cenozoic and modern faunas is greater than that characteristic of Paleozoic dominant groups. Passive, suspension-feeding, epifaunal and shallow infaunal modes of life characterized much of the Paleozoic fauna. More active life habits—deep burrowing, swimming and predation—became widespread as more ecospace was utilized by the expanding modern fauna. Many replacement groups have higher average metabolic rates than the Paleozoic groups they replaced, as would be expected for organisms with increasingly active life styles.

For example, Thayer (1981) called the sedentary, passive, suspension-feeding articulate brachiopods "minimal organisms" and pointed out the variety of ways in which articulates function with low energy expenditure. In contrast, as well as supporting more living tissue, bivalve mollusks are more active. Many move around, even if sluggishly, some burrow actively, and some scallops can swim.

The contrast extends to metabolic rates. Peck et al. (1989) reported that, for individuals of equivalent biomass under similar physical conditions, the oxygen consumption rate for the articulate brachiopod *Terebratulina retusa* (L.) is only 12% that of the byssate bivalve *Mytilus edulis*. Thayer (1992) argues that the low energy requirement of articulate brachiopods accounts for their continued abundance in low food supply (oligotrophic) environments while bivalves dominate in more food-rich habitats. Rhodes (1992) and Rhodes and Thompson (1993) have documented that some brachiopods actually stop feeding activity when cell concentrations in the water are at levels bivalves regularly utilize.

The contrast between passive and active life habits is also expressed in the shift in dominant echinoderms. The blastozoans and crinoids of the Paleozoic were all attached suspension-feeders whereas the abundant echinoids of the Cenozoic are mobile. Two abundant and diverse groups of echinoids have extended their activity to burrowing. The most abundant modern group of crinoids, the comatulids, has even abandoned attachment and become mobile, crawling on cirri and, in some cases, even swimming.

Increase in Particularly Energetic Modes of Life

Active burrowing deposit-feeding and predation are two especially energetic general modes of life. It takes a constant expenditure of energy to dig through the sediment searching for food, as deposit-feeders and infaunal predators do. Predators must be more active and spend more energy than the lower-level consumers they eat because they must search for, catch, and subdue their prey. Both deposit-feeding and predation existed in the early Paleozoic, but were uncommon. Both became progressively more widespread later in the Paleozoic but neither reached their peak until the Cretaceous and Cenozoic.

Active Infauna.—Active, deep-burrowing infauna have increased in diversity, abundance and range of habitat (Crimes 1974; Seilacher 1974) as part of the general increase in utilized ecospace above and below the sediment-water interface during the Phanerozoic

(Bottjer and Ausich 1986; Ausich and Bottjer 1990). The progressive spread of deep infaunal activity in time and space is revealed by changes in the depth and intensity of bioturbation preserved in sediments of different ages (Bambach and Sepkoski 1979; Larson and Rhoads 1983; Thayer 1983; Brandt 1986; Sepkoski et al. 1991).

Although deep-burrowing (30 cm to 1 m) infauna had evolved by the Early Cambrian, they were abundant only in shoreface sands, tidal flats, and shallow nearshore environments (Miller and Byers 1984; Simpson 1991). However, on average, shelf sediments in the Cambrian were only slightly reworked, normally to depths of only 2–3 cm (Droser and Bottjer 1988). Bioturbation in shelf environments progressively increased from the Cambrian to Ordovician (Droser and Bottjer 1989) and again from the Ordovician to the Devonian (Larson and Rhoads 1983). Burrowing depths of 5–6 cm became common in the Devonian, reaching 30 cm in some settings. Devonian style bioturbation persisted through the rest of the Paleozoic and into the Triassic (Aigner 1985). The intensity of both rate and depth of bioturbation increased dramatically in shelf environments in the Mesozoic, as extensively documented by Thayer (1983). Thinner event beds (less than 3–4 cm thick) virtually disappear from the post-Triassic geologic record because of disruption and homogenization by bioturbation (Brandt 1986).

The expansion of active infauna includes suspension-feeders, which live rather passive lives, but also includes numerous deposit-feeders and predators, both of which spend energy digging or burrowing continuously through the sediment to obtain food. But infaunal suspension-feeders must be more active than attached or sedentary epifauna because they need to reburrow or reestablish connection with the overlying water mass when disturbed. Sediment reworking by deposit-feeders and scavengers is so energetic today that Clifton (1971) found that as many as half of the 1200 shells (ranging in length from 20 to 80 mm) he placed on the Caribbean sea floor in areas undisturbed by wave or current action were turned over and half were buried in just forty days. Sediment distur-

bance by “biological bulldozers” (Thayer 1979) is now so severe that LaBarbara (1981) concluded that some reclining free-living bivalves which were abundant in the later Mesozoic, such as *Gryphaea* and *Exogyra*, would not be able to survive on the modern sea floor. The increase in infaunal activity through the Phanerozoic clearly has required the burning of more calories as time has gone on.

Predation.—Predation has increased through time (Vermeij 1977; Signor and Brett 1984; Brett 1990—and more specialized studies: Carter 1967; Sohl 1969; Taylor et al. 1980; Vermeij 1983; Kabat 1990). The history of predation begins with possible predatory borings reported from the Late Precambrian (Bengston and Zhao 1992). The spectacular genus *Anomalocaris* (Briggs 1979; Whittington and Briggs 1985) and the diversity of priapulids preserved in the Burgess Shale (Conway Morris 1977) are ample evidence that predators had evolved by the Middle Cambrian. Nonetheless, evidence of predation is quite rare until the Devonian. Starfish are present by the Ordovician, but they were not nearly as flexible and capable of wrapping around bivalve prey as they became in the Mesozoic and Cenozoic. Cephalopods are abundant after the Late Cambrian, but no preserved jaw structures (rhyncholites) are known with certainty before the Carboniferous (Gasirowski 1973), although Alexander (1986: p. 279) found a possible rhyncholite actually imbedded in an Ordovician brachiopod valve. Even some of the presumed evidence of early Paleozoic predation, such as some of the cylindrical borings in Ordovician brachiopods that resemble predatory gastropod borings (Carriker and Yochelson 1968), have turned out to be post-mortem features (Richards and Shabica 1969). Predation becomes more evident in the mid-Paleozoic, and the fossil record of obvious predators improves as well (Signor and Brett 1984). The mid-Paleozoic spread of a variety of anti-predator and predation resistant morphologies reflects the impact of increasing predation pressure on prey organisms. The Mesozoic saw further diversification of predators (Vermeij 1977), including the radiation of infaunal predators (Thayer 1983). During the Cretaceous and early Cenozoic, predatory

mechanisms (e.g., drilling, shell crushing) were elaborated in great variety as the caenogastropods, crabs, echinoids, and teleost fish all diversified explosively. Vermeij (1977) called this radiation of predators and its coevolutionary response among prey organisms the Mesozoic marine revolution.

Increased intensity of predation has accompanied the progressive diversification of predators, implying that the abundance of predators also increased. Despite the existence of some predators before the Devonian, evidence of active predation is rare in the early Paleozoic and predation intensity was, on average, quite low. Bengston and Zhao (1992) report that 2.7% (14 of 524) of the tubes from Shaanxi Province, China, of *Cloudina*, the oldest known skeletonized fossil, have cylindrical bore holes apparently made by a predator. Alexander (1986) recorded shell breakage related to predation for nine genera of brachiopods from the Late Ordovician in the Cincinnati Arch area. Two showed virtually no effects of predation and six had from four to ten percent damaged valves. One, a concavo-convex form (*Rafinesquina*), had 26.4% of the valves damaged, but 81% of the damaged valves had been hurt at less than 27 mm length and the predation was not very effective (most of the damaged specimens survived to grow larger). At larger sizes (up to 50 mm) shell fracture by predators was much reduced. Chatterton and Whitehead (1987) reported that in one bed from the Silurian of Oklahoma up to 10% of the valves of an inarticulate brachiopod have small predatory borings, but none of the valves were bored in a bed 1 m higher in the section. In my dissertation collection of 14,000 bivalve specimens from the Silurian of Nova Scotia, I found no bored specimens and no crushed shells that could be differentiated from crushing by sediment compaction.

Average predation intensity definitely increased in the Devonian, but it was still far below late Mesozoic and Cenozoic levels. Buehler (1969) notes that only 45 of 2000 shells (2.25%) of a Devonian brachiopod were bored perpendicular to the shell surface in typical efficient predatory fashion. Sheehan and Lespérance (1978) found 11.2% (14 of 125) of the

valves less than 17 mm in size of an Early Devonian brachiopod from Quebec were drilled but none of the larger specimens had drill holes. By the Carboniferous shell crushing by fish can be demonstrated. Alexander (1981) observed predatory shell crushing scars in brachiopods from the mid-Carboniferous (Chesterian) of Utah. The percentage of scarred shells ranges from 3.4% to 22.5%. Bruton (1966) also observed shell crushing in Vissean fossils from Northern Ireland and he reported possible predator borings in as many as 30% of the valves of some brachiopods. My current work in the Pennsylvanian suggests that the rate of boring seen by Bruton is much higher than normal for the Late Paleozoic. Mapes et al. (1989) report shark inflicted injuries on Pennsylvanian conularids. In a classic study on taphonomy in a Permian assemblage, Boyd and Newell (1972) did not see predatory boring in shells, although there were numerous small post-mortem borings, but they found 20% of the shells of one species of bivalve and 25% of the shells of another had been fractured, presumably by predatory fish.

Vermeij (1987) summarized the record of the increase in predation intensity by calculating the percent of species with more than a specified level of recorded predatory attack in assemblages of different ages. Shell repair frequency doubled during the Mesozoic. A mean of 25% of the species in Carboniferous and Triassic assemblages show evidence of shell repair in more than a quarter of their specimens but a mean of 52.5% of the species in Cretaceous and Cenozoic (including recent) assemblages show evidence of shell repair in more than a quarter of their individuals. In Neogene assemblages, shell boring by gastropods and shell crushing by crabs have been added to previously established predatory strategies. For example, drilling increased dramatically after the Cretaceous. Fifteen percent to thirty percent of species in Cretaceous assemblages have 10% or more of their individuals drilled but 25%–95% (mean of 56% for 11 assemblages studied) of species in Cenozoic assemblages have 10% or more of their individuals drilled (Vermeij 1987). Shell boring alone was responsible for the

mortality of 3%–30% of the specimens in different species of Miocene mollusks from Oregon (Colbath 1985), 25%–30% of glycymerids from the Miocene and Pliocene of eastern North America (Thomas 1976), 3%–74% of different Miocene species from the Chesapeake Group (Kelley 1991) and 10%–60% of the different species in a Pleistocene deposit in Mexico (Stump 1975). This contrasts with no drilled bivalve shells in the Silurian and only 2%–11% (and one report of 30%) later in the Paleozoic.

Predation is an energetic mode of life and the survival of predators depends on abundant energy acquisition. Kitchell et al. (1981) demonstrated that predatory gastropods actually select and manipulate prey to maximize net energy gain and Kelley (1991) demonstrated that naticid cannibalism even fits such a cost–benefit analysis. The increase in predation over time indicates that more calories are being spent in the fauna with the passage of time. Because the survival of predators requires an adequate biomass to support them, the increase in the number of predators over time suggests that the biomass of prey must have increased to support them.

More active life habits and higher metabolic rates require more nutrition. It is apparent that the modern fauna, to support both higher biomass and more energetic modes of life, requires more food and energy than did the Paleozoic fauna.

More Effective Exploitation or More Resources?

The acquisition of more food and energy by the modern marine fauna could be an intrinsic result of more effective use of unchanged food resources, or the tapping of previously unutilized food reservoirs, or the result of an increase in supply of food in the marine ecosystem.

Constraints on Increased Effectiveness

Constraints on the degree of possible change in effectiveness of function exist in any group, as can be seen by considering the three aspects of Seilacher's analytic approach to "*konstruktions-morphologie*" (Seilacher 1970; Raup 1972). The phylogenetic heritage of ge-

netic potential and developmental program (*historisch-phylogenetischer aspekt*) channels all organisms in a group into particular pathways. They cannot become what their genome cannot provide. Trilobites remained trilobites; teleosts are teleosts. On top of this, the physical constraints of strength of materials and rates of reactions are fixed by the properties of the materials organisms are able to use in growth and development. This structural aspect or morphogenetic program (*bautechnischer aspekt*) is confining, too. Calcite and aragonite will never be hard enough to abrade quartz or the feldspars. Both the phylogenetic and structural aspects limit the range of evolutionary change a group of organisms can achieve without developing adaptive modification of the Bauplan of the sort that usually characterize new higher taxa. The necessities of adaptation to specific environments (*ökologisch-adaptiver aspekt*) is the selective component in the system. Here effectiveness in utilizing resources can be improved, but, because selection is ever present where competitive conditions exist (Darwin 1859), any "improvement" will take over quickly (on a geological time scale), and, because of the historical and structural constraints inherent in any Bauplan, the optimal realizable effectiveness of any mode of life in a group is quickly achieved. For example, the feathers of the earliest bird, *Archaeopteryx*, which has other more avian characters than previously recognized as well (Prokop et al. 1988), were already fully adapted for the aerodynamic function of flight (Feduccia and Tordoff 1979).

The fact that species packing within guilds has not increased over time (Bambach 1983) illustrates how little change in effectiveness of resource utilization occurs after a group, or a mode of life adopted by members of a group, becomes established. As a specific example, no change in resource partitioning was found over a 400 m.y. span in a comparison of Silurian and Recent bivalve dominated deposit-feeding communities (Levinton and Bambach 1975). The end result is that once a general mode of life is developed in a group it does not seem to continuously "progress" but remains at the level of effectiveness it

reached as the group became established. When a group does appear to develop greater effectiveness it is almost always associated with an evolutionary innovation that permits greater utilization of ecospace. For example, skeletal plate reduction permitted starfish to increase flexibility, changes in tooth form in the lantern of echinoids opened up possibilities for new feeding activity, such as predation, and a shift in the position of the anus from the top of the test to the posterior interambulacral area accompanied the development of infaunal modes of life in echinoids. Most change of this magnitude is recognized in traditional taxonomy at the ordinal level (Bambach 1985; Bambach and Sepkoski 1992). Morphologic breakthroughs, not gradual change, are associated with increases in utilization of ecospace (Bambach 1985). Constraint on change in effectiveness in resource utilization permits generalized comparison of groups through time by analogy with their general properties in the Recent.

Different groups do have different ecologic potentials, however. The shifting balance of dominance among the varied taxa changes the ecologic context in which organisms find themselves. It is this changing ecologic context through time that results in escalation (Vermeij 1987) and the operation of the "Red Queen" (Van Valen 1973).

Some of the dominant groups in the modern fauna are more effective at food acquisition than were Paleozoic dominants. Bivalve mollusks and other mucus-sheet suspension-feeders are highly effective at removing suspended material from the water and brachiopods are less so (Rhodes 1992). But this does not mean the turnover in faunal dominance and the increase in biomass and energetics in the modern fauna is simply a product of the new dominant groups taking a larger portion of an unchanged food resource. The survival of the descendants of Paleozoic dominant groups in oligotrophic refugia is probably because food supplies in such settings are so low that modern dominants, despite their greater feeding effectiveness, cannot get adequate nutrition to out-compete the low-energy-budget remnants of Paleozoic dominants. These relict Paleozoic dominants

require so little food that they obtain adequate nutrition even under low food supply conditions and they can still dominate such habitats today (Thayer 1992).

Because constraints exist on the increase in effectiveness of resource utilization once a group becomes established, it is not likely that increase in biomass within long established groups was attained simply by more effective use of already exploited resources. Instead, it appears that the resource base was enlarged and the carrying capacity of the ecosystem expanded.

The Need for More Food to Fuel Expansion

Biomass of the benthos is positively correlated with primary productivity in surface waters (Degens and Mopper 1976; Thiel 1983). Nutrient supply from the land, nutrient recycling in estuaries, lagoons, and coastal waters, and coastal upwelling all make near-shore productivity higher than on the shelves or in the open sea (Raymont 1980). Maps of primary productivity for the world ocean illustrate this clearly (Berger and Wefer 1991: p. 1908), as do plots of biomass with distance from shore and increasing depth (Rowe 1983b). All dominant classes in the modern fauna (and many orders) have existed since the Ordovician. In the Paleozoic, abundant occurrences of now dominant taxa were generally restricted to shoreline and inner shelf settings (Sepkoski and Miller 1985) where food would be expected to be relatively abundant, but those same taxa are now widespread in all habitats. If adequate food had existed during the Paleozoic across the range of habitats now dominated by the modern fauna, why didn't the members of the modern fauna already extant live abundantly in the same range of habitats then as they do now? On the other hand, the remnants of some of the Paleozoic faunal dominants, which were widespread in all habitats then, are common only in oligotrophic refugia now (Thayer 1992). This argues strongly for an increase in food supply as a major factor in the expansion of the modern high biomass fauna. The following examples all independently point to

an increase in food supply to marine consumers during the Phanerozoic.

Expansion of Deep Deposit-Feeding.—A major share of homogenizing bioturbation is contributed by deposit-feeders (Thayer 1983; Jumars and Wheatcroft 1989). Although it was of limited facies extent, deep burrowing associated with deposit-feeding is present in the Cambrian (Miller and Byers 1984: p. 42) in shoal, nearshore settings. I have seen similar thickly bioturbated beds in very nearshore strata in the Ordovician (*Orthorhynchula* Zone of the Martinsburg Formation on Walker Mountain in Virginia), in the Silurian of Nova Scotia (parts of the Moydart Formation and the Lower Stonehouse Formation, below and above the "Red Band," a non-marine stratum) and in the Devonian in eastern New York (in the very nearshore and shoreface facies of the Hamilton Group in the area of East Berne, Rensselaerville, and Alcove, southwest of Albany). As discussed above, the extent of deep burrowing bioturbation has expanded over time and is now common in many environments. Since deposit-feeders capable of deep burrowing were already in existence in the early Paleozoic why didn't they rework shelf sediments as they do today?

Deposit-feeding has "substantial energetic cost" (Jumars and Wheatcroft 1989). Deposit-feeders won't burrow deeply into sediments unless there is enough buried food to make it worthwhile. A particularly interesting example of the probable relationship between food supply and the limitation of deep burrowing in deep-water sediments is one of the exceptions to the general restriction of Early Paleozoic deep burrowing to shallow nearshore facies. Burrows penetrating 40 cm or more vertically occur in a setting interpreted as a levee or interchannel area on a submarine fan system in the Cambrian(?)–Early Ordovician age Meguma Group of Nova Scotia (Pickerill and Williams 1989). The burrows are quite dense near a 2 m deep submarine channel, decrease in abundance away from the channel and are entirely absent 5 m laterally from the channel wall. As Pickerill and Williams note, one possible reason for the association of these deep burrows with the channel form is that food resources may have

been brought down the channel from shallow water. Waterlogged organic matter is commonly swept down submarine canyons and onto submarine fans in the modern ocean. This example illustrates the point that food limitation, not water depth or distance from shore, controls the distribution of deep burrowing deposit-feeding infauna.

The time lag between the origin of deep deposit-feeders, which originally inhabited only areas known to have the highest productivity and food supply, and the expansion of their range into shelf settings suggests that an increase in buried food is responsible. The pattern of progressive increase in the depth of active bioturbation through the Phanerozoic, beginning in the early Paleozoic (Droser and Bottjer 1988, 1989; Larson and Rhoads 1983) and culminating in the Mesozoic (Thayer 1983), probably maps the increase in food supply. Because decay after burial limits the depth at which enough labile material remains to serve as an adequate food resource (Walker and Bambach 1974), more supply would be necessary to have some edible food remain after deep burial. Of course, reworking would also stir organic matter into the sediment, enhancing the rate of burial, but enhanced circulation of fluids into and out of burrows would also increase the potential for oxidation and decay (Aller 1982).

The abundance of organic carbon in marine sediments correlates positively with primary production and inversely with grain size, water depth and supply of diluting sediments (Calvert and Pedersen 1992). Because the range of sedimentation rates, grain sizes, and water depths should remain about the same throughout the Phanerozoic, an overall increase in organic content of sediments should reflect a general increase in primary productivity. Can we document an increased flux of food (organic material) to the sea floor over time?

The distribution and abundance of petroleum source rocks come to mind as a possible source of data on changing productivity through time, but they do not monitor average global conditions or average secular change through time. Petroleum source rocks are generally deposited only in regions of

high productivity. For instance, Parrish (1982a,b) found a highly significant correlation of the distribution of petroleum source rocks with upwelling zones modeled on paleogeographic reconstructions for both the Paleozoic and the Mesozoic–Cenozoic. The degradation of the rock record with time from tectonism and erosion also prevents a quantitative evaluation of change in the volume of organic rich sediments through time. It is not possible to differentiate a secular signal from the basic phenomenon of loss of record with time which produces an artifactual impression of increase toward the recent (Gregor 1985).

Jackson (1975) measured the concentration of a suite of organic materials he called “humic” matter (interpreted as diagenetic alteration products of algal pigments and lipids) in sediments ranging in age from 3.4 Ga to 16 Ma. He reported an increase in content of humic matter in sediments throughout geologic time with a sharp apparent rise in the Phanerozoic. Four Cambrian and Ordovician samples (two shales and two limestones) contained a range from 0.8 to 34 (mean of 13.2) ppm humic matter, four Late Paleozoic samples (two shales and two limestones) had a range of 6 to 2570 (mean of 690) ppm humic matter, and three Cretaceous and Cenozoic shales had values of 1680, 27,400 and 29,400 ppm humic matter. Unfortunately, as Van Valen (1976) also noted, the data set is very small and the variance in the data is great. Also, the two high value samples from the Cenozoic are both from “bioproductites” (the Eocene Green River Formation and the Miocene Monterey Formation) and would be expected to have unusually high concentrations of organic material. However, Jackson did analyze potentially organic rich sediments from earlier times; the only Early Paleozoic shales were the Cambrian Burgess Shale, famous for its preservation of unskeletonized organisms, and a graptolitic black shale from the Lower Ordovician; the Late Paleozoic samples included the organic-rich Devonian Antrim Shale and Permian Kupferschiefer. Considering this, it is interesting that three of the four Late Paleozoic samples contained higher

concentrations of humic matter than three of the four Early Paleozoic samples and the lowest value of the three Cretaceous–Cenozoic samples (the Cretaceous Pierre Shale) had more than an order of magnitude higher concentration of humic matter than all but one of the Late Paleozoic samples and all of the Early Paleozoic samples. Although we cannot use these data as a statistically sound measure of increase in organic material in marine sediments, the general pattern and the comparison of less extreme values in the data set are both consistent with an increase in the supply of organic matter to marine sediments during the Phanerozoic.

The increase in buried organic matter suggested by the expansion of deep burrowing deposit-feeding and Jackson’s data on humic matter might have occurred because suspension-feeders declined and took less of the organic matter settling at the sediment–water interface, rather than because food supply increased, but this is not the case. Instead, an expansion of suspension-feeding also occurred in the Paleozoic, with suspension-feeders developing tiering above the sediment–water interface as well as persisting in abundance at the sediment–water interface (Bottjer and Ausich 1986; Ausich and Bottjer 1990). In the Mesozoic, siphonate suspension-feeding bivalves expanded into the fauna, too (Stanley 1968).

Tiering in General.—While not arguing that increasing food supply was the cause of increased epifaunal tiering of suspension feeders, it is obvious that epifaunal tiering couldn’t have developed if adequate food weren’t available. Even if food supplies had not increased, the benthic fauna would have exploited more volume of habitat for food as tiering increased (Bottjer and Ausich 1986; Ausich and Bottjer 1990), thus increasing the total nutrient supply utilized by benthic organisms. Food is most densely concentrated at the sediment–water interface and normally decreases in amount down into the sediment (as decay depletes the labile fraction of the buried organic matter) and up into the water mass with distance from the boundary layer where resuspension occurs (Walker and Bam-

bach 1974). Tiering above the sediment surface could have developed simply to capture suspended food resources unutilized by organisms on the bottom, but the increase in tiering both above and below the sediment-water interface, coupled to the persistence of an abundant benthos at the sediment surface, implies that food supply to the bottom increased through the Phanerozoic. If it had not, the development of effective suspension feeders tiered up into the water column should have strained much food out of the water column and also removed a large amount of resuspended food before either settled to the bottom. This would have reduced food supply to the low-level benthos and the infauna, limiting those modes of life. Yet they persisted and, in the case of the fauna, increased at the same time epifaunal tiering increased.

Expansion of Trace Fossil Diversity in Deep-Water.—The diversity of trace fossils in deep-water environments has increased through time (Crimes 1974; Seilacher 1974). Crimes' tabulation of ichnogenus diversity for the *Nereites* (deep water) community lists three ichnogenera in the Cambrian (none in the Precambrian), nine in the Ordovician and Silurian, an average of twelve from the Devonian through Jurassic, and thirty in the Cretaceous and Cenozoic. I report Crimes' numbers to present the overall pattern shown by a consistent data set, but more recent work has increased the total number of ichnogenera recorded in deep-water communities. For example, Pickerill and Keppie (1981) report 11 ichnogenera in the Cambro-Ordovician deep-water Meguma Group in Nova Scotia, and Pickerill (1980) recorded 23 ichnogenera from the flysch in the Ordovician Aroostook-Matapedia Belt in New Brunswick. However, the overall pattern of deep-water trace fossil diversity has not changed from sequence of Cambrian low, Ordovician to Jurassic medium and Cretaceous-Cenozoic high diversity reported by Crimes. Pickerill (1980) points out that the Cambrian has "consistently low" deep-water trace fossil diversity, and that "the carrying capacity was drastically increased" in the Cretaceous. Sampling in paleontology

will always be incomplete but we apparently do have a sufficient sample to be confident of the general shape of most diversity patterns (Sepkoski 1993).

Kitchell et al. (1978) noted that in an abyssal region with low surface productivity (the Arctic Canada Basin) the diversity of recent trace forms was very limited (three species) but trace diversity was high (20 species) in an abyssal region (the Antarctic Bellingshausen Basin) which was four orders of magnitude greater surface productivity than the Arctic Canada Basin. The high diversity at 2100 meter depths along the U.S. mid-Atlantic continental slope (Grassle and Maciolek 1992)—798 species, including 385 annelids, identified from 233 box cores taken at 14 stations—is actually found at the depths of the slope where export from the shelf, surface productivity, and sedimentation combine to produce the highest organic matter content in sediments found along the entire shelf to basin transect (Premuzic et al. 1982). The modern deep-sea has very low food supplies and deep basins far from land are so devoid of food that diversity, as well as biomass and organism density, is reduced (Rex 1983).

Trace-fossil makers were already diverse in shallower environments in the Cambrian, so the restriction on diversity in deeper-water deposits in the early Paleozoic cannot be just slow diversification of the varied behavioral patterns ichnogenera represent. Crimes lists 24 ichnogenera in shallow communities in the Cambrian, as many as for any period in the Phanerozoic, and 13 ichnogenera independent of depth in the Ordovician, within one of the maximum in that category. Because low food supply is known to be associated with low diversity of deep-sea trace makers in the Recent and a diversity of trace-fossil making organisms already existed in shallow-water settings with greater access to food input in the early Paleozoic, it is probable that the increase in deep-water trace fossil diversity through the Phanerozoic has been tied to an increase in the food supply to food-limited deep-water habitats. Food supply in the Cambrian may have been so low it limited diversity in deep basins, as it does in the abyss

in the center of oceanic gyres today (Rex 1983). As surface productivity and food supply to deep water increased, the diversity of deep-water traces also increased. The increases in deep-water diversity match the timing of biomass and energetic increase suggested for the shelf biota.

Bivalve Mollusks and Carbonates.—Bivalve mollusks were generally more diverse nearshore than offshore throughout the Paleozoic, but they were not restricted to inshore conditions (Miller 1988). Bivalves were present in all parts of the gradient from the shoreline to deep basins and they became fairly diverse in off-shelf habitats at several times after the mid-Devonian. However, when clastic and carbonate environments of deposition are considered separately, the two sediment types display a sharp difference in the pattern of bivalve diversity in space and time (Miller 1988). In clastic settings high bivalve diversity was restricted to nearshore environments only in the mid-Ordovician to mid-Silurian. After that, while bivalve diversity was often somewhat higher nearshore, fairly high diversity was attained in mid-shelf and deep settings and even developed at times in outer shelf habitats. On the other hand, bivalve diversity in carbonate depositional environments remained very low in mid-shelf, outer shelf, and basinal settings from the Ordovician into the Early Permian. Until the Late Permian, when intermediate bivalve diversity finally developed across the spectrum of carbonate shelf habitats, bivalve diversity in carbonates was high only in nearshore settings. Except for deep-burrowing siphonate suspension-feeding, the full range of bivalve adaptive strategies had developed by the Silurian (Bambach 1971). The restriction in habitat range for bivalves in carbonates cannot be because needed adaptive strategies had not yet evolved. Why did bivalves attain high diversity only in nearshore carbonate environments during most of the Paleozoic if they had a full range of modes of life available and could live in most clastic settings?

Clastic sediments are transported by current flow from land source areas to wherever they are deposited. Therefore, all clastic depositional settings have an external input of

both particulate matter and material in solution. Nutrients or food can adhere to particle surfaces and transporting currents can bring nutrients or light organic food particles, especially if they are transporting clastic sediment away from the high-food-concentration coastal zone, through which all clastic sediment must travel at some point. But carbonates form in situ. To be sure, carbonate sedimentation is a result of biological activity, but productivity in carbonate environments need not be high. The rate of deposition of carbonates is commonly very slow compared to the rate of clastic accumulation. In fact, carbonate formation by benthic productivity is inhibited by reduced light penetration in areas where high water fertility permits the growth of abundant phytoplankton, causing increased turbidity. The difference in bivalve diversity in clastics and carbonates in offshore settings during most of the Paleozoic may reflect the difference in food supply for bivalves in the two sedimentary regimes. The spread of bivalves into the full spectrum of carbonate environments at the end of the Paleozoic may reflect increasing primary productivity and food supplies in previously low food supply regimes.

Crinoid Filtration Systems Then and Now.—The fact that fine-filtered (pinnulate) crinoids reach an energy deficit at higher current velocities than do coarse-filtered (non-pinnulate) crinoids (Baumiller 1992) presents a conundrum. Kammer and Ausich (1987) found that current velocity played a role in the environmental distribution of pinnulate and non-pinnulate forms in the Mississippian, with pinnulate forms commonest in higher current velocity settings. Non-pinnulate forms had broader environmental tolerances and were the dominant forms in low current velocity habitats by default. The surviving crinoids, the Articulata, are pinnulate and yet are found in a wide range of habitats, from high current velocity settings in reefs to quiet abyssal habitats. How can the passive stalked forms found in abyssal settings survive in low-current-flow deep waters if the filtration fan has a high flow resistance? These animals, by rights, should have low flow resistance (non-pinnulate) filters since the high resis-

tance filter, while able to intersect widely dispersed particles, passes less volume of fluid at low current velocities than does a low flow resistance filter, making feeding more difficult at low flow rates. Baumiller points out that the muscular arm articulation of the Articulata allows more morphologic flexibility. This may permit the animals to adjust flow resistance to fit current velocity better, as Kammer and Ausich suggested for the densely branched but non-pinnulate arms of the flexible crinoids of the Mississippian. Or, there may be more food particles in suspension now, even in abyssal settings, than there were in quiet water conditions in the Paleozoic and the increased flux of food particles may make up for the greater resistance of flow through the pinnulate filter. Baumiller also notes that the pinnulate cladids, the ancestral group to the Articulata, had a wide range of environmental tolerance in the Paleozoic. Were the quiet water occurrences of these fine-filtered crinoids in settings that might have had higher food concentration than normal?

Predators and Biomass.—The increase in predation is a powerful argument for the increase in biomass at the base of the food chain. Because the efficiency of energy transfer is about 20% between primary producers and marine herbivores and detritivores and between 10% and 15% between each higher trophic level (Parsons et al. 1984) it is necessary that five to ten times the biomass (and energy content) of the consuming group must be available for consumption at each level of the food chain to support the next higher level. This is why food chains only extend to six or seven steps on our finite-sized earth. Great white sharks and killer whales are the ultimate marine predators. It also means that any increase in biomass of predators requires a concomitant proportional increase in the biomass of the prey—and in the biomass at each supporting step of the food chain down to, and including, primary production.

Cropping by predators can limit the standing crop biomass of prey (Paine 1966; Woodin 1981; Parsons et al. 1984) and herbivores can reduce the standing crop biomass of primary producers (Steneck 1983). Cropping has been cited as a method of raising diversity by pre-

venting competitive exclusion by cropped organisms (Paine 1966). The cropping phenomenon also has been suggested as having had a role in the Cambrian radiation (Stanley 1976) and in changing algal floras through time (Steneck 1983; Estes and Steinberg 1988). As discussed above, the abundance of dominant organisms in the predation-intensive Cenozoic is at least as great as it was in the more benign early Paleozoic and is probably even greater. The record of increasing biomass through time has accumulated against the increasing potential for biomass consumption from predation. This underscores the idea that food supplies have increased considerably over time. Increase in food availability for prey organisms has enabled production of prey to support the expansion of predation through the Phanerozoic and increase the standing crop biomass of prey as well.

The great diversification of predators in the late Mesozoic and Cenozoic incorporated much refined trophic niche subdivision through the development of specialized predatory mechanisms and strategies (Kohn 1959; Vermeij 1978). To permit each specialization by a predator, an adequate biomass of appropriate prey organisms that could be effectively caught by that specialized mechanism or strategy had to be available; and, obviously, enough biomass in appropriate prey must be continuously available to permit a specialized predator to continue to exist. The diversification of numerous specialized caenogastropods and brachyurans in the Late Cretaceous and Cenozoic attests to the buildup of higher biomass in many different types of prey. All those prey had to eat more to support their growing biomass; their food supply must have increased, too.

The Evidence of Increased Productivity

Given the increased biomass and increased energetics of the modern fauna compared to the Paleozoic fauna and the evidence that these changes have been supported, at least in part, by an increase in food supplies, it seems incontrovertible that primary production has increased to support the expansion and escalation of life activities in the marine

realm. Fortunately, there is good evidence that this has occurred.

Life on Land

Land Plants.—The evolution and radiation of vascular plants is the most obvious evidence of increased productivity on a global scale during the Phanerozoic (Niklas et al. 1985; Edwards and Burgess 1990; Collinson 1990). Except for some thin lichens and some microscopic prokaryotes, there was no biomass on the land and little productivity until the rise of the vascular plants. For all practical purposes the entire bulk of vascular plants is added biomass and all their productivity is new productivity added during the Phanerozoic.

The expansion of plants on the land began in the Mid- to Late Ordovician with the change from a thin covering, at best, of lichens on rock surfaces and bacteria and algae in moist areas to the first hints, from spores and cuticle-like material, of possible ancestors of tracheophytes. Primitive vascular plant types diversified during the Silurian, but all were still small and limited to moist habitats. None reached more than a meter in height until the Late Early Devonian (Emsian). Tree-size lycopods evolved in the Middle Devonian and the biomass of land vegetation began to build significantly. The late Paleozoic is characterized by the expansion of numerous plant groups. Dramatic evidence of large scale productivity is preserved in the accumulation of Carboniferous coals. This burst of productivity had global impact and contributed to major changes in atmospheric oxygen (increased) and carbon dioxide (decreased) (Bernier and Canfield 1989; Bernier 1991). Gymnosperms and other plant groups capable of life in drier habitats radiated in the Permian and Triassic, expanding the area of the land covered with vegetation. The highly productive angiosperms originated in the Early Cretaceous and radiated from the mid-Cretaceous into the Cenozoic. All the surface of the earth with enough water to sustain plant life became covered with living tissue.

Consequences of Land Plant Evolution.—One of the functions of vascular plants is to strip nutrient cations out of the rocks beneath the

land surface and pull them out of the ground (in solution in their vascular tissues) so they can react with atmospheric gases in the light from the sun. This puts these inorganic nutrients into labile organic matter and, upon the death of the living tissue, leaves them loose on the ground.

Robinson (1990a,b) reports that fungally mediated decay has increased markedly since the Paleozoic. She contends that this change has influenced the rate at which organic matter has been buried on land. Without basidiomycete activity lignin-rich plant tissue resists biological decay and accumulates in soils. The increase in decay by fungi reduced the proportion of terrigenous organic production buried on land, thus speeding up the organic-carbon cycle on land and keeping the oxygen content of the atmosphere relatively stable as plant productivity increased in the Mesozoic and Cenozoic. Enhanced decay also aided in the release of nutrients from dead vegetation.

Land plants and their activity, especially the penetration of roots, which release organic acids and also physically disturb the regolith, into the soil and weathering rock and the accumulation in the soil of organic matter, which releases carbon dioxide as it decays, increase weathering rates dramatically (Ollier 1984; Krumbein and Dyer 1985; Knoll and James 1987; Schwartzman and Volk 1989; Volk 1989). The changes wrought by plants on rock weathering are preserved in the changes in soils through time (Retallack 1986; Wright 1990).

The buildup of land vegetation and its biomass supported the diversification of terrestrial invertebrates (Selden 1990; Shear 1990; Labandeira and Beall 1990), which began in the Late Ordovician (Retallack and Feakes 1987), and vertebrates (Padian and Clemens 1985; Benton 1985), beginning in the Devonian. The animal biomass also mobilizes and redistributes nutrients, leaving them more accessible for transport by physical surface processes.

Impact on the Marine Ecosystem

Has the growing productivity on land and its effect on increased weathering rates and nutrient mobility had an impact on the ma-

rine ecosystem? Land plant ecosystems retain and recycle nutrients very effectively and it has been argued that the evolution of land vegetation has decreased nutrient supply to the oceans (Tappan 1982, 1986). However, recent evaluation of nutrient retention and nutrient leakage from terrestrial ecosystems reveals that, although nutrients are retained in immature forest ecosystems still adding biomass, mature ecosystems with a stable biomass lose nutrients in runoff at rates equivalent to the weathering rate itself (Lewis 1986; Schlesinger 1991). Mature systems are, in effect, steady state systems and cannot retain more nutrients than they are supplied. Although most vegetated areas on earth today are not in steady state equilibrium because of human disturbance, this was not true for most of geologic time. In the past, when most of the land area of the earth supported undisturbed, mature plant communities, nutrient export to the sea in runoff would have equaled weathering rate and nutrient supply to those communities. Since land plants enhance weathering rates, the supply of nutrients to the sea, compared to the unvegetated early Paleozoic, would have become greater as more effective vegetation cover evolved.

The transport of nutrients from the land to the sea is a complex process. Limiting nutrients are not directly exported. Nitrogen and phosphorus are recycled through phytoplankton in streams and estuaries (Lewis 1988; Jordan et al. 1991). These processes may alter the balance of nutrients arriving in open coastal waters from those that left the community from which they were initially derived. In the transition from a watershed to an estuary in Maryland, Jordan et al. (1991) found biological processes continued to extract phosphorus from sediments, enriching the phosphorus content of estuarine water compared to the river water, but nitrogen was reduced although still present. Although nutrients may be trapped and recycled in estuaries this is, over geologic time, not an issue because estuaries are always temporary features. Nutrients will be supplied directly to coastal waters when estuaries are sediment filled. Stored nutrients in estuarine sediments will be flushed out when sea level drops and

estuarine fills are eroded and transported to the marine environment. The end result is that runoff from the land leads to "a general enhancement of nutrients in estuaries and in coastal waters influenced by land drainage" (Burton 1980: pp. 310-311).

Runoff from vegetated land areas also brings organic material to the coastal environment in detrital, colloidal and dissolved form. The role of plant detritus is complex (Mann 1988); it serves as a substrate for bacterial floras, becomes a food resource when partially degraded, and supplies dissolved organic matter which is also utilized by organisms. The biological conditioning of coastal waters by humic materials favors high phytoplankton productivity (Prakash 1971). Nutrient export from the land to the sea takes place in the atmosphere, too. Coastal phytoplankton production is stimulated downwind of land masses by nitrate from rain (Paerl et al. 1990) and wind-blown dust is believed to be the dominant source for iron (a limiting nutrient for cyanobacteria and possibly some eukaryotic phytoplankton) in the photic zone of the sea (Duce and Tindale 1991). Concentrations of trace element nutrients near continents are usually adequate for phytoplankton growth but are limiting far from land (Schlesinger 1991).

The result of the input of nutrients from land is that estuarine and coastal productivity is far higher than most of the open sea (Schlesinger 1991). Satellite imagery, identifying wave-length reflectance from chlorophyll, reveals two orders of magnitude or more higher density of phytoplankton in coastal waters of the eastern North Atlantic than beyond the continental shelf.

Coastal productivity is not the end of the story, however. Although there is much nutrient recycling in the coastal region, it, too, loses material seaward. Offshore Ekman transport, resuspension by surface waves on the inner shelf, and resuspension by tides and internal waves on the outer shelf all combine to move organic material to the shelf margin where it becomes available for downslope movement into the deep sea (Walsh 1989). Walsh estimates that half the particulate carbon reaching two km water depth is derived

from continental margins. Decay in coastal regions also puts nutrients into solution and tidal exchange and currents mix them into the oceanic water mass.

Productivity on the land has a direct impact on marine productivity. Vegetation speeds weathering rates and its decay mobilizes nutrients. Runoff from the land supplies nutrients to the coastal zone, and may do so at the rate of weathering when the land vegetation is mature and stable. Organic material in runoff enhances phytoplankton productivity, too. Estuarine, coastal and shelf processes recycle nutrients, thus adding to the support of higher biomass, but the coastal region also leaks and a significant amount of organic matter and nutrients in the open sea is derived from the coastal setting. Clearly change in land vegetation influences the whole system. The increase in vegetation on land over time has increased the supply of nutrients, in both rate and volume, to the sea.

Marine Phytoplankton

Increase in the diversity and abundance of marine phytoplankton and increase in the volume of sediment generated by marine phytoplankton is evidence for an increase in marine productivity through the Phanerozoic. Vidal and Knoll (1983) summarized information on plankton in the Proterozoic and earliest Cambrian, and Tappan and Loeblich (1973) compiled species diversity data for the major groups of plankton through the Phanerozoic. Although more species have been described in the last twenty years, experience with a variety of data compilations on diversity made at different times reveals that patterns of diversity change are very robust, remaining similar in all but detail in all reasonably comprehensive data sets (Valentine 1969; Sepkoski et al. 1981; Sepkoski 1993). The Tappan-Loeblich data set is the most comprehensive yet compiled for marine phytoplankton at the species level for the whole Phanerozoic and its general patterns can be trusted. The pattern of total phytoplankton diversity through the Phanerozoic follows a familiar pattern, except for the late Paleozoic—low in the Vendian and Early Cambrian (a maximum of 30 Early Vendian species,

a few more than 40 in the later Early Cambrian), rising to a Paleozoic maximum in the Ordovician through Devonian (300–400 acritarch species), a diversity drop in the late Paleozoic and early Mesozoic, a rise in the Jurassic and Early Cretaceous to 400 or so species (of a diverse suite of acritarchs, dinoflagellates, calcareous nannoplankton and diatoms), and finally a burst of growth in diversity in the Upper Cretaceous to over 1000 species with high diversity persisting through the Cenozoic (1350 Pliocene fossil species and 6440 living species).

If abundance and productivity at least crudely follow diversity, then we have a general monitor of changing productivity in the oceans through the Phanerozoic. We do have a check on productivity for the Jurassic through Cenozoic in the record of accumulation in the deep sea of biogenic sediment produced by phytoplankton. For this interval the blossoming of productivity that parallels the increase in diversity is unambiguous. Wilkinson and Walker (1989), comparing a series of models for carbonate deposition in the deep sea with the mass-age distribution as preserved, established that productivity in the late Mesozoic was not comparable to that in the modern ocean. Therefore, it is not unreasonable to think that Paleozoic phytoplankton diversity variation also parallels productivity. The low Early Cambrian diversity suggests that productivity was also low. It rose into the Ordovician and remained relatively steady into the Devonian. Fewer than 100 acritarch species are recorded from any interval from the Carboniferous through the Triassic. This long interval of low diversity in preserved phytoplankton is puzzling, especially since suspension-feeding benthic invertebrates flourished in Carboniferous and Early Permian shallow seas. As Tappan has suggested, it could reflect nutrient reduction due to the remarkable buildup of biomass on the continental platforms, especially in the coal measures of the Carboniferous, but that seems like an unusually long interval to keep the land vegetation from attaining some level of stability. However, the remarkable sea level oscillations that created Late Carboniferous and Early Permian cyclothem, plus the range

of environmental and biotic changes around the Permo-Triassic boundary, may have kept the land vegetation in a protracted state of flux. Detritus from the land vegetation may have helped to maintain an adequate food supply for shelf faunas. On the other hand, the diversity of acritarchs remained quite stable from the Early Carboniferous into the Paleogene. That doesn't suggest great instability. Another possibility is that some rarely preserved group flourished. Many algal groups do not produce mineralized or decay resistant organic parts and are rarely preserved. For example, Tappan and Loeblich (1973) mention that prasinophyceans, although always low in diversity, occur in high abundance in some late Paleozoic strata and they note that chlorophycean green algae are found sporadically in rocks of every geological period from the Mississippian to the present.

The late Paleozoic interval of low preserved phytoplankton diversity may be puzzling but, in the context of this paper, it is a perturbation, not a Phanerozoic length trend, and it shouldn't distract from the main goal, determining overall pattern. For this, the general oceanic phytoplankton picture is clear. The order of magnitude rise in acritarch diversity from the very low level of the Early Cambrian to hundreds of species in the mid-Paleozoic speaks of a shift from very low to higher productivity levels and the Jurassic to Cenozoic increase, from species diversities comparable to the mid-Paleozoic to the high diversity of the Cenozoic, when combined with study of the accumulation rates of biogenic sediments in the deep-sea, unambiguously documents the major Cretaceous-Cenozoic increase in productivity.

The radiation of diverse eukaryotic phytoplankton (e.g., coccolithopores, dinoflagellates, diatoms) in the Cretaceous and Cenozoic has implications for oceanic productivity in another sense. Brand (1991) has established that cyanobacteria are nutrient limited by the low concentration of usable iron rather than phosphorus or nitrogen in surface waters far from land. Eukaryotic phytoplankton species, however, display very different Fe:P ratios in iron depleted regions

than those in iron rich nearshore settings. It seems eukaryotic phytoplankton species inhabiting open sea environments have evolved the ability to get along with less iron. Phosphorus, which is more abundant than iron in the open sea, is the limiting nutrient for them. This is an example of a breakthrough in function in newly diversified groups which has permitted an increase in productivity in the marine ecosystem, in this case by reducing the need for a potentially limiting nutrient. This breakthrough may have triggered the radiation of the eukaryotic phytoplankton in the late Mesozoic, permitting an increase in primary productivity in the open ocean with little change in the supply of trace nutrients.

Conclusions

The increase in fleshiness and in average size of individual common organisms plus the increase in thickness and abundance of shell accumulations, indicating at least constant and possibly increased numbers of individuals, points to an increase in the biomass of marine consumers during the Phanerozoic. Increases in metabolic activity, both as basal metabolism and as increase in more energetic modes of life, argues that the expenditure of energy by marine consumers has increased with time as well. Although groups that have risen to dominance in the Mesozoic and Cenozoic may exploit resources more effectively than Paleozoic dominants, the increase in effectiveness has constraints and does not explain all the changes through the Phanerozoic. The time lag in expansion of more energetic life habits from environmental settings of known higher food supply into regions of expected lower rate of food supply (bivalves into offshore carbonate depositional environments, deep burrowing deposit-feeders into the spectrum of shelf environments) and the time lag in the diversification of energetic modes of life (predation, deep-sea trace fossil makers) for long intervals after they originated suggest that the supply of food increased across the whole spectrum of marine habitats during the Phanerozoic. The great diversification of specialized predators especially suggests that biomass increased all the way down the food chain to the level of

primary production. The increase of plant life on land, coupled to the impact that land vegetation has on stimulating productivity in coastal marine settings, and the transfer of material from coastal regions to the open ocean, plus the increase in diversity and abundance of phytoplankton, all point to an increase in productivity in the oceans through the Phanerozoic.

These conclusions seem to run counter to several arguments, or at least possible interpretations of arguments, advanced in the past about the relationship of diversity to nutrients and biomass and about the impact of the diversification of land vegetation on the marine ecosystem. Valentine (1971) argued that highest diversity develops in stable, resource poor (oligotrophic) settings. The increasing diversity during the Phanerozoic might then be associated with a decrease in food resources, not an increase. Stanley (1976) argued that cropping by herbivores may have permitted the diversification of metazoans by reducing the competitive exclusion that might have ruled the previously ecologically stable, algally dominated world "essentially analogous to highly eutrophic modern systems." From this one might assume that the continued diversification of life could also have been driven by further cropping as herbivory and then carnivory became common, and that more intense cropping could have limited total biomass. Tappan (1982, 1986) has argued that the expansion of land vegetation has led to the sequestering of nutrients on land and a progressive reduction of nutrient supply to the marine ecosystem. She argued that this had controlled many events in the evolution of the marine biosphere and may have been responsible for the great mass extinctions of the Phanerozoic, which coincide or overlap in time with major expansions of biomass on land.

The problem with Valentine's theoretical argument turns out to be that his model was incomplete, although he based it on the known data of the time. Valentine compared just two systems of resource supply, rich and poor (Valentine 1971: p. 57), using diversity data from deep sea studies (which he acknowledged were sparse and inconclusive) in developing his physically stable, low re-

source, high diversity model. Those preliminary deep sea data suggested that the food-poor deep sea was more diverse than the food-rich shallow shelves. Now we know that the highest diversities are at 2–3 km depths on the lower continental slopes and upper continental rises (Rex 1983; Grassle and Maciolek 1992), where organic matter from the shelf as well as that settling from surface productivity first arrive in the deep sea. The highest concentration of organic matter in surface sediments along the transect from shelf to ocean basin center occurs at these depths in the western North Atlantic (Premuzic et al. 1982). Diversity decreases from these depths down to the 4–5-km depths of the abyssal plains and broad ocean basins, which are truly food poor because they are both further from land and at greater depths where there has been more opportunity for consumption and decay of organic matter settling from the photic zone. Diversity follows an arch-like path as it rises from lower values on the shallow shelves to a high point at mid-depths and then falls again to values similar to shallow areas or even less in the deep basin expanses (Rex 1983: p. 458–459). The complete explanation for the reduction of diversity going into the deeper parts of ocean basins is not fully understood, but one factor involved seems to be that food is just too scarce. Biomass per unit area unambiguously decreases, by about four orders of magnitude, with increase in depth down to 4 km and then remains nearly the same at all greater depths (Rowe 1983b). Decreasing food supply is a known part of that change. Valentine's model is still reasonable, but a third level, resource inadequacy, should be added to it. The history of the marine biosphere through the Phanerozoic is probably development from the level of resource inadequacy in the Early Cambrian, which may have had even lower food resources in outer shelf and basinal settings than the modern abyss, to the diverse resource levels of the modern oceans, but where truly eutrophic conditions are still quite restricted in extent.

Stanley (1976) did not argue that the Proterozoic world was eutrophic in the modern sense of high nutrient supply and excessive productivity creating environments choked

with excess biomass. He only argued that it might have been analogous in the sense that a few producers were utilizing all the available resources. He explicitly noted that there was probably lower nutrient input and lower productivity in Proterozoic aquatic systems (Stanley 1976: p. 214). But if a reader skips the disclaimer and extends the model to the logical end, then the misimpression could be formed that diversification, through cropping, might even reduce biomass over time. At the low nutrient and productivity levels that probably characterized the Late Proterozoic, algal growth may have utilized all available nutrients until the first herbivore evolved. The cropping phenomenon could have been a trigger for the diversification of metazoans, but later events have increased nutrient supplies, productivity and biomass. Cropping events on a local scale, however, can still be part of the system.

Tappan (1982, 1986) built a theoretical argument before the more recent data on nutrient export from mature land communities (Lewis 1986; Schlesinger 1991) were available and without dealing with the details of consumer biomass, energetics, and habitat expansion dealt with in this paper. Changes in land vegetation probably have influenced nutrient supply to the oceans from time to time, especially when biomass was increasing on land or productivity was being sequestered, as in the formation of extensive coals, but these changes would be perturbations on the general pattern. This paper is an attempt to describe general change from the Paleozoic to the Cenozoic and does not try to account for all the perturbations along that path, important and interesting though they be. The overall picture of the buildup in diversity of marine consumers and its relationship to increase in biomass and energetics seems robust. The coincidence of the match with the expansion of land vegetation and its impact on the marine ecosystem, as we now understand it, suggests that those events are connected by positive, not negative feedback, over the span of the whole Phanerozoic.

As Tappan points out, carbon in the biomass of the marine realm is a very small proportion of the world total of organic carbon, some 0.06% (Tappan 1982, 1986). Many un-

certainities still exist concerning the mechanisms and rates of transfer of carbon between reservoirs (Berger et al. 1989; Longhurst 1991) with some error bars ranging up to 50 to 100%! Small changes in rates and processes could shift carbon flow to enlarge the minuscule size of the living marine biosphere over time without being obvious, or even easily detectable in general geochemical analyses, given the uncertainties in flow rates and reservoir sizes. The patterns noted in this paper, however, are directly empirical and describe what we know happened to marine consumers during the Phanerozoic. In every case these patterns point in the direction of increase through the Phanerozoic in biomass, energetics and supporting food supply. Such seems to be the story of seafood through time.

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