

PALEOSCENE #10. Paleocology: paleoecosystems, paleocommunities

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PALEOSCENE #10. Paleoecology: paleoecosystems, paleocommunities

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Third fisherman: "Master, I marvel how the fishes live in the sea"
First fisherman: "Why, as men do a land, the great ones eat up the little ones"
(William Shakespeare)

Introduction

In our solar system, Planet Earth is unique and distinct by its possession of a living, growing, reproducing and biogeochemically recycling envelope, the *biosphere*. Some 100 billion metric tons of organic matter are produced on Earth each year, a relatively fragile, yet extremely tenacious and constantly dynamic, changing, evolving film of living tissue, which, if spread out evenly over the globe, would be less than 0.1 mm thick. It is very likely this living film developed only because Earth is close enough to the Sun not to be a frozen planet and yet far enough away not to have its oceans evaporate. More recently, some have looked on Earth as a single organism, Gaia, with its rivers and oceans acting as its salty bloodstream, its atmosphere as its lungs and the biosphere as its tissues and organs (Lovelock, 1979). Moreover, it is further suggested that this single organism has a mammalian, built-in thermostat, having regulated its own "body" temperature for the last 3.5 billion years, the salinity of its bloodstream and the oxygen, nitrogen and carbon dioxide content of its lungs. There is reasonable evidence to assume that the bloodstream of our planet underwent a radical conversion some 600 Ma ago to produce a phosphate-enriched ocean (Cook and Shergold, 1984) with a salinity of about 35 ppt and a pH of about 8, and, an atmosphere of about 2.0% oxygen (the minimum required to sustain the metabolic activity of skeleton-secreting meta-zoans). This self-regulating Earth "organism" has developed its own checks and balances, and, like other life more familiar to us, has evolved through time.

Paleoecology (from the Greek *palaio*, ancient, *oikos*, dwelling place, *logos*, study of) is the study of the relationship of ancient organisms to their planetary environment, and how these organisms functioned within their habitat and toward each other. It has sometimes been divided into the study of groups of organisms (*paleosynecology*: usually the study of communities) and the study of individual organisms or parts thereof (*paleoautecology*: usually functional morphology). As a subdiscipline of paleontology, paleoecology is relatively new. The first textbook *Introduction to Paleoecology*, by the Russian paleontologist Roman Gekker, appeared in 1957 (English translation, 1965); the first English text was by Derek Ager (1963). Since then no really comprehensive text has appeared, although there are a number of edited compilations covering limited subjects [see book list]. In the past, fossils were studied primarily for two reasons. The first was to reveal the nature of extinct life (the monographic taxonomy of lineages), and the second was for the stratigraphic (and economic) usefulness of fossils as markers or keys to the geologic record, i.e., biostratigraphy. In the last 20 years, however, it has come to be realized that fossil species did not live in splendid isolation but were part of complex units in the environment, and that fossils might provide remarkable clues to wide-ranging processes which have shaped our planet in the past. In a nutshell, *paleoecosystems* might be defined as units ["black boxes"] of naturally associated "fossil" organisms which once functioned together, interacting with the physical-chemical environment [the abiotic component] to produce a *dynamic flow of energy*, a specific *trophic hierarchy* [the food chain], *species diversity* and a *cycle of*

materials [biogeochemical cycles]. Ecosystems are not static: they constantly evolve and perfect themselves, adapting to a planet itself undergoing constant change through the major geological processes of plate tectonics. At the largest end of the scale, our whole planet represents one ecosystem. At the smaller end, the gut of a marine clam, an algal mat on an intertidal substrate, or a hollow tree trunk, could be considered an ecosystem.

Energy flow

Since ecosystems are characterised by energy flow, what are the primary sources and paths of this energy? The most abundant single source of energy, the fuel for ecosystems, clearly is the Sun, which provides both light for *photosynthesis* and is the driver of the ambient climate, wind and ocean currents. Volcanoes, geothermal heat and gravitational processes are minute in their relative energy impact on the biosphere. Some stored chemical energy is available to specific organisms, mostly bacteria, which derive their energy directly from the breakdown of atomic bonds (*chemosynthesis*). Ultimately, of course, the earth's crust, with its storehouse of raw materials, has provided both water and the basic building blocks of organic molecules: carbon, oxygen, hydrogen, phosphorus, nitrogen and sulphur. These materials are not available in equal abundance in the lithosphere, hydrosphere, atmosphere and biosphere, and must be derived from one to pass to another. Most of the world's organic carbon is stored in limestone, with only a fractional amount available in dead organic matter on land and at sea (and in fossil fuels: coal, oil and gas) and even smaller proportions available in living matter (Figure 1: Bolin, 1970).

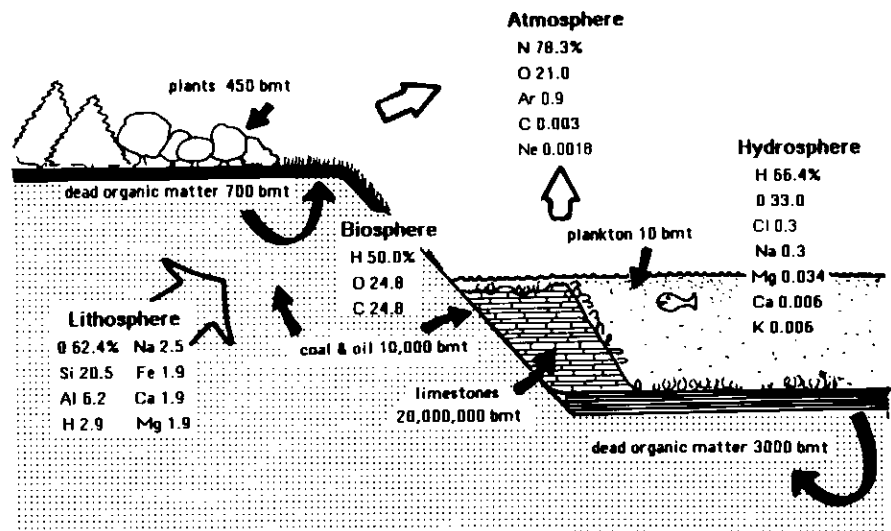


Figure 1 Cycling of elements from a biosphere perspective. Note the concentration of carbon in the global ecosystem, most of which is stored in limestones (20,000,000 billion metric tons, bmt). Contrast the live organic production on land (450 bmt) with that at sea, a virtual "desert" (10 bmt), but the far greater amount of storage in the marine environment (3000 bmt) versus that on land (700 bmt). This may be explained largely via erosion, which is dominant on land, and deposition, which dominates at sea.

For much of earth's history, the most efficient mechanism of energy transfer from the sun to the biosphere has been the process of photosynthesis, with free oxygen being a by-product of the process along with the organic carbon. This began with the evolution of cyanobacteria [the "blue-greens"] more than 3500 million years ago, recorded in the geological record as stromatolites. There is general agreement that initially the photosynthetic cyanobacteria, and later eucaryotic red and green algae (about 1700-1400 Ma), were the prime agents responsible for producing a weakly oxygenic atmosphere in the Precambrian (see Raup and Jablonski, 1986). Chemosynthetic archaeobacteria, which can operate without sunlight and under extremely harsh conditions, were perhaps the first living organisms (even preceding the cyanobacteria). These possibly lived at deep sea hydrothermal vents, in muds of tidal flats, lakes and ocean floors or in brine-enriched hot springs or salt flats of terrestrial habitats (Nisbet, 1986).

Cycling elements

There is a constant interaction between organisms and the chemical elements within their environments and a constant play between organisms and the physical controls of their environment (e.g., temperature, light, moisture, etc.). In *allogenic*, or externally manipulated ecosystems, with very strong physical controls, e.g., deserts, the organisms are the tolerated guests of the habitat. But, in biologically highly complex *autogenic* ecosystems, such as the coral reef or the tropical rain forest, the organisms are the hosts: they immediately control the physics and chemistry of their habitat and provide an equilibrium. In the fore-reef zone, algae and corals modulate wave energy, pump oxygen into the system at the reef crest by creating turbulence, create the substrate and provide a buffer zone for more fragile organisms in the back reef. In the equatorial rain forest, tree canopies control evaporation and humidity, baffle the wind and dampen light, creating cooler sub-zones, while root systems and soil decomposers recycle the nutrients.

The three most important constituents of living cells are C, H and O, which constitute 99.6% of organic matter. The remaining critical elements, in order of declining abundance, are N, Ca, K, S and Mg. A quick glance at the importance of C in the lithosphere shows that it is a scarce planetary resource (Figure 1). Thus all biogeochemical cycling hinges around C, the main reservoir on earth by far being limestones, derived from oceans, and a secondary source being the atmosphere. Carbon becomes available to life through photo- and chemosynthesis, with carbon dioxide now largely derived from the erosion of limestones, respiration and fermentation. The original source of C was either the lithosphere, or, as has been suggested more

recently, the bombardment of earth by carbonaceous chondrites. Much of the early carbon, nevertheless, was probably released during early stages of crustal formation with extensive degassing of the cooling mantle producing a carbon dioxide-rich atmosphere. The evolution of photosynthesis was thus a major step in changing atmospheric conditions.

Life has been described as a "choreography of the sea's elements". In fact, at least over the last 1500-2000 Ma, with the atmosphere becoming weakly oxidizing, life has acted as a focal point for most surficial chemical cycles (see Holland and Trendall, 1984). The sea appears to have maintained its basic, present salinity, pH and elemental geochemistry since the arrival of the pre-Tommotian and Tommotian shelly fauna in Cambrian time (Holser, 1984): it was at this stage that world-wide biomineralization occurred in a wide-ranging group of marine algae, primitive metazoans and more advanced sponges, coralline elements and shelly calcareous and phosphatic organisms (Fisher, 1984; Brasier, 1986; Leadbeater and Riding, 1986). Four of the five kingdoms of organisms (Margulis and Schwartz, 1982: the monerans, protocists, fungi, and animals) were present in the late Proterozoic ocean. The last one, the vascular plants, probably arrived in the Middle Ordovician, or, at the latest, by about mid- to late-Silurian time (Chaloner and Lawson, 1985; Retallack and Feakes, 1987). It has been estimated that in the Early Cambrian there may have been as many as 50 classes of marine organisms, although the affinities of these with various phyla are still in dispute.

Recycling of materials is an essential factor in ecosystems. Without recycling, or, in a different light, life without death, carbon would soon be depleted unless there was a

very high, constant rate of erosion and/or large-scale volcanism or degassing (the last three features appear typical of primitive ecosystems in the Precambrian). It can be seen that if organic matter was precipitated around the globe even at the rate of 0.01 mm per year, the geologically short time span of the Pleistocene (ca. 2.3 Ma) would see the whole earth covered in 23 m of plant and animal matter. This does not happen, simply because nature is very efficient at recycling its own garbage through the activity of decomposers, carnivores, detritivores, coprophagites and scavengers (Figure 2).

Respiration almost balances photosynthesis: most protocists and higher animals obtain their energy for self-maintenance by absorption ("burning") of oxygen to produce carbon dioxide, water and cell matter. Anaerobic respiration is practiced by bacteria, fungi and some protocists. Decomposition, the breakdown, usually of animal tissues, by bacteria, and of plant matter by fungi, is probably volumetrically more important than respiration as an oxygen converter. Many animals help the decomposition process along, e.g., the scavengers and detritivores. All these energy transfer mechanisms, photosynthesis, respiration and decomposition, have relatively low efficiencies in nature. Normally less than 10% is transferred from one step to the next, and more than 90% is lost. Energy is lost in searching for food, maintaining body (cell) heat, respiration and reproduction. Ecologists can measure energy gains and losses through ecosystems by calculating productivity in terms of gram weights or kilocalories per unit area per unit time. Geologists at best can only approximate biomass productivity over very rough time units by calculating growth rates or quantitative abundance on bedding planes (Staff *et al.*, 1985).

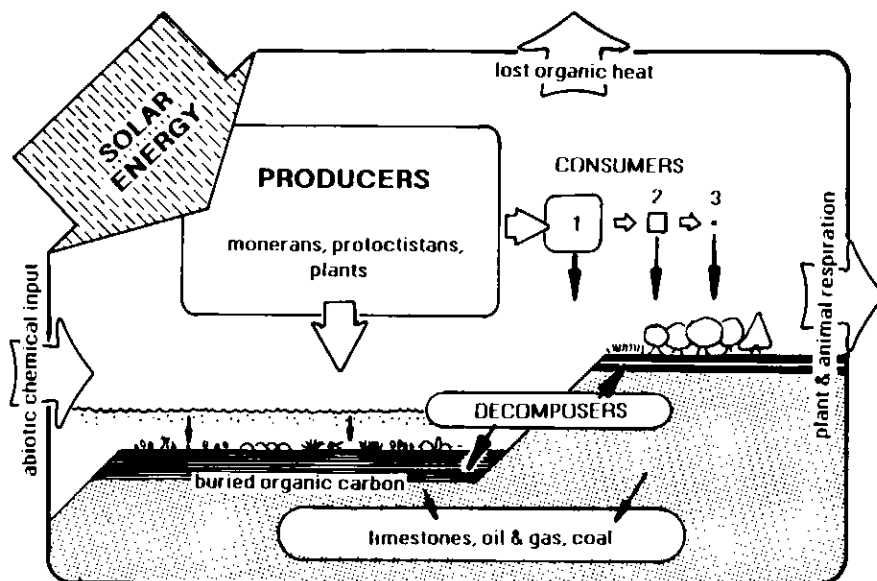


Figure 2 Energy flows through ecosystems and food chains via producers and consumers, with organic matter recycled by decomposers. The remainder is stored as dead organic matter (fossil fuels, limestones, etc.) or lost as gases or heat.

Trophic structure: food chains and food webs

Trophic structure (Greek, *trophe* = food, nourishment) refers to the feeding interactions between organisms and their environment. Normally this is considered in terms of food chains, food webs and food pyramids. A *food chain* is a linear relationship with A eating B, B eating C, etc. A *food web* refers to the more complex, natural situation in nature where one consumer may eat several types of prey at several levels of the food chain. A *food pyramid* is a diagrammatic device intended to show that the base of the food chain has the greatest biomass, numbers of organisms or energy production rate, and the top of the food chain, the least. Feeding is basically an energy transfer mechanism. In simplest terms, organisms can be divided into *autotrophs*, those which convert elements or compounds into organic matter using solar or chemical energy (e.g., cyanobacteria, algae, vascular plants using photosynthesis, or bacteria using chemosynthesis), and, *heterotrophs*, those which rely on other living or dead things for their nourishment (e.g., carnivores, herbivores, detritivores, planktivores, etc.: Figure 2). Some organisms may be *partial heterotrophs*, living symbiotically with autotrophs to gain some of their energy, supplementing that with grazing, suspension or detritus feeding. It has been suggested that the earliest metazoans, which belong to the mouthless and gutless Ediacara fauna, may have been *diffusion feeders*, osmotically pumping oxygen and dissolved organic nutrients through expansive membranous walls (Runnegar, 1982), and that these may also have been photoautotrophs using algal symbionts (Seilacher, 1984; McMenamin, 1986), thus accounting for their large surface areas.

Alternatively, the Ediacara biota may have had photosynthetic and chemosynthetic symbionts, the latter like the deep sea, hydrogen sulphide dependent invertebrates (Jannasch, 1984). Stanley (1973) has suggested that, until herbivores evolved, trophic levels in communities were self-limiting, and that establishment of a food chain led to the explosive evolution of life at the beginning of the Phanerozoic.

Another way of looking at trophic structure is to divide the roles into *producers*, those which manufacture their tissues from simpler materials (microphytoplankton dominate at sea, the vascular plants on land), and *consumers*, those which eat other living things, dead matter or their wastes. A third category normally employed is that of *decomposers*, the "garbagemen" which break down pre-existing organic matter, such as bacteria and fungi, and recycle the elements for re-use by the producers. All three are essential for maintaining the ecosystem. Partial heterotrophy and photoautotrophy represent combinations of producers and consumers, while diffusion feeding reflects simple osmotic exchange of nutrient chemicals.

Lumping all consumers into a single category is not a useful exercise since it tells us little about the complexities and energy loss down the *food chain*. As a result, consumers have usually been split up into smaller units identifying the food types consumed and the nature of the feeding process. Moreover, the levels at which food is consumed have importance because there are limits to the length of the food chain. At each level, with an energy loss of 90% or more, there are strains on those surviving at the upper level, such as the larger carnivores. It has been noted that the "supercarnivores" (giant sharks, whales, etc.) occur sporadically

through the geologic record during periods when global diversity is high and climates warm (Fischer and Arthur, 1977). The ways which Nature has developed to cope with the energy loss at the higher trophic levels include by-passing steps in the food-chain (some whales developed gigantic straining mechanisms for filtering plankton), having organisms vary their diet so that they can lunch at different levels to get all their mineral supplements (as in most food webs) or varying food intake at different times of the year or at different stages in growth.

The base of the marine food chain in most instances appears to be and to have been phytoplankton, benthic algal mats and macrophytic algae (seaweeds) and, more recently, angiosperms (sea grasses). On land, the primary source of food today is the vascular plants, mostly the angiosperms. Algal mats, seaweeds, sea grasses and the terrestrial leafy plants are consumed by herbivorous grazers and browsers, thus producing a *grazing-browsing food chain* (Figure 3). In aquatic environments, the first level consumers appear to be dominated by suspension-feeding organisms which tackle the microscopically sized phytoplankton (monerans and protoctists) and/or microzooplankton, or may take in suspended dead organic matter (together these are called the *seston*). Consumption of these leads to a *suspension feeding food chain* (Figure 4). A third type of food chain, the *detritus feeding food chain*, may also be of considerable importance, for there is abundant nutrition available in organic detritus found on sea floors, tidal flats, lake and river bottoms and in the soil environment (Figure 5). It has been suggested that detritus feeding may have acted as a buffer to Cretaceous extinction on land as well at sea, allowing the regeneration of more complex food chains following mass extinction phases that decimated the herbivorous dinosaurs and killed off the phytoplankton (Sheehan and Hansen, 1986). A *photoautotrophic-diffusion feeding system*, such as that suggested for the Late Precambrian metazoans, would not in the strict sense be a food chain because it would have lacked grazing and browsing herbivores and carnivores and simply consisted of producers and decomposers.

Not all food chains base their primary resource on photosynthetic autotrophs. The exception to the rules includes examples such as the *chemoautolithotrophic*, bacterially based food chain we may observe in the deep sea (Figure 6). At active "smoker" vent systems, or on passive margins, where oil and gas seeps provide the necessary hydrogen sulphide to stimulate bacterial productivity, benthic organisms such as polychaete worms, crustaceans, tube worms and clams and companion carnivores thrive (Somero, 1984; Jannasch, 1984). The tube worms and clams carry on a symbiotic relationship with sulphur-oxidizing, procaryotic bacteria (the

GRAZING—BROWSING FOOD CHAIN

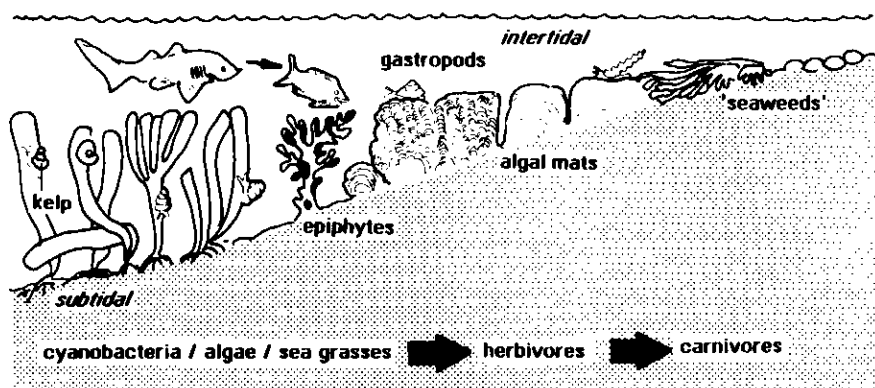


Figure 3 The grazing/browsing marine food chain. This is normally initiated by benthic herbivores such as snails or other invertebrates and vertebrates (herbivorous fish). Grazing is the normal term for those that live on algal or cyanobacterial mats, while browsing is the term conferred on those that consume the "leafy" algal macrophytes or sea grasses. Such food chains normally occur in very shallow environments, including the intertidal zone. Grazing is thought to have started at the beginning of the Cambrian, causing a rapid decline in preservation of subtidal, normal marine algal mats (stromatolites), which were then confined to hypersaline habitats which deterred the grazers. Subtidal stromatolites continued, but nearly exclusively as skeletalized forms (e.g., Girvanella, Epiphyton, Renalcis, etc.).

tube worm *Riftia* has no ingestive nor digestive system). Bacterial chemosynthesis drives the whole vent ecosystem: this has been suggested as a model for earliest Precambrian life, prior to the evolution of photosynthesis (Corliss *et al.*, 1981).

When did these food chains become established? It is clear that for most of Earth history, the Precambrian, no "true" producer-consumer food chain existed. The land areas were relatively barren and the oceans featured simple autotrophic, prokaryotic monerans and protocists, commonly in the form of algal mats (preserved as *stromatolites*), which, upon death or destruction would be recycled by decomposer bacteria. Phytoplankton may have been introduced into the upper layers of the oceans with the advent of eucaryotes between 1900-1400 Ma (these required oxygen, the oxygen then providing an ozone shield which would have protected surface plankton from ultraviolet light). The fossil record of the oldest eucaryotes is disputed: cell spots, larger sizes and tetrads have all been taken as evidence for a nucleated cell, but degradation of cyanobacterial tissue can produce remarkable nucleus look-alikes. Undisputed is the presence of acritarchs in rocks as old as 1400 Ma (Knoll, 1983), suggesting the presence of surface-dwelling plankton no later than this time.

The picture changed in the late Precambrian (Ediacaran) interval which began about 900 Ma ago. Prior to this time there are no unequivocal metazoan fossils, though some have been reported (*e.g.*, Kauffmann and Fürsich, 1983). The Ediacaran world, which saw the explosive development of the first soft-bodied metazoans, has been explained in two ways. The first view suggests that this fauna was dominated by heterotrophic detritus feeding marine worms and by suspension feeding cnidarians such as seapens and jellyfish, and other early invertebrates (Glaessner, 1984). Many polychaetes and non-skeletal coelenterates are known to tolerate very low oxygen levels and large surface areas may have improved oxygen uptake. Some Ediacaran "seapens" and "flatworms" reached sizes of 1 m or more. If this view is correct, both detritus and suspension food chains were established at this time. The presence of simple trace fossils in the late Precambrian does not tell us anything at present about detritus feeding or grazing: such ichnia may represent locomotion unconnected with the search for food. The second, more recent, view of the Ediacara fauna interprets these shallow water metazoans as photoautotroph-diffusion feeders, thus eliminating heterotrophy such as suspension or detritus feeding as a factor (see McMenamin, 1986). Again, this would then not be a true food chain, since only producers and decomposing bacteria would be present. Knoll (1983) has suggested that vase-shaped microfossils found in the late

Precambrian (ca. 800 Ma, *i.e.*, Ediacaran) represent the most ancient "micro-predators" because of their similarity to heterotrophic tintinnid ciliates. If that interpretation is correct, then at the microbial (and plankton?) level food webs might have been more complex than at the metazoan level. Whatever the explanation, it is clear that the introduction of mobile animals in the late Precambrian marked a radical departure from early, simple methodology in nutrient uptake and reproductive strategy.

The widespread appearance of skeletalization in biotas of the Early Cambrian, including the producer calcareous "algae" (cyanobacteria, red and green algae) and a large number of exotic invertebrate consumer

classes, had a major impact on food chains in marine environments. In fact, new feeding techniques, such as herbivory and carnivory, may have stimulated the explosive introduction of protective phosphate, carbonate and silica secretion of skeletons or reinforcing spicules in prey organisms (Stanley, 1976). In turn, the evolution of hard structures, such as teeth, pincers, claws and reinforced legs, would have improved success in grazing, in detritus feeding and in carnivory. Additionally, "bulldozing", the biological disturbance of sediment (Thayer, 1979), was almost certainly enhanced by the development of hard parts.

It is evident that skeletalization was not a global, simultaneous event in all groups:

SUSPENSION FEEDING FOOD CHAIN

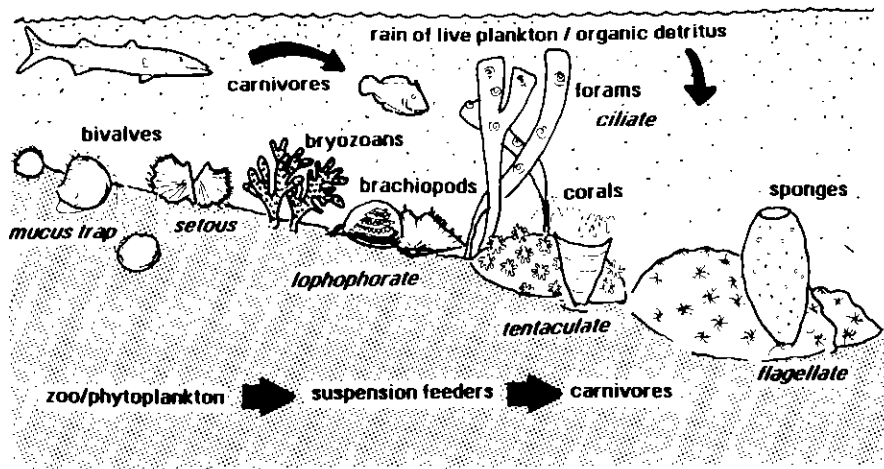


Figure 4 Suspension feeding food chains. Marine environments of the Paleozoic appear to have been dominated by suspension feeders, most of which were benthic, sessile invertebrates. These subsisted presumably on live zoo- and phytoplankton in the water column, but may also have consumed a substantial amount of dead organic detritus available in the same water mass. Many built supporting or protective skeletons. Corals were "awaiters" which may have been both carnivores and suspension feeders. Feeding types cited are highly variable, some being selective.

DETRITUS FEEDING FOOD CHAIN

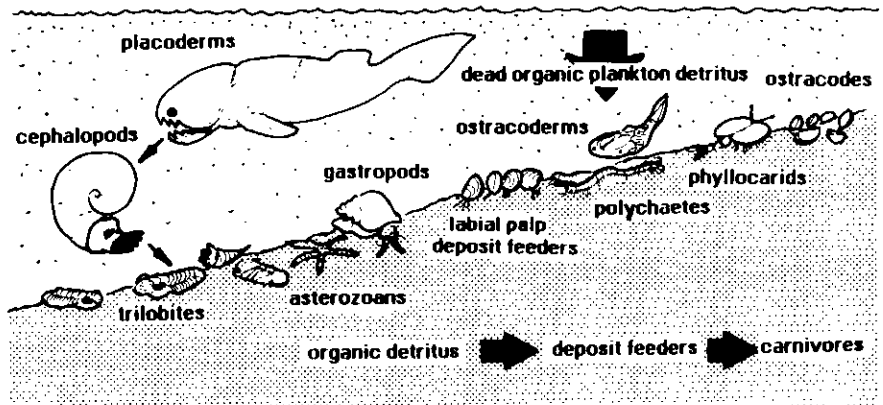


Figure 5 Detritus feeding food chain. This is dominated by vagile benthic animals, including many soft-bodied forms. Examples shown are those which might be typical of a Devonian sea bottom. Infauna are not shown, though these include many deposit feeders (for infauna see Figure 8). The ostracoderm shown was probably a detritus feeder: the oldest, jawless fishes of the Cambrian and Ordovician appear to have been detritus feeders that vacuumed the substrate for food resources.

trilobites, for example, appear later than the small Tommotian shelly fossils. And, it now seems probable that global changes in ocean geochemistry may have been a major stimulus toward skeleton production at the end of the Precambrian (Cook and Shergold, 1984; Fischer, 1984; Brasier, 1986). It is probable, considering the large diversity of invertebrate classes, that *grazing, suspension and detritus feeding* all appeared in relatively short order in shallow marine environments in the late Vendian (Late Precambrian) or no later than the basal Cambrian, thus establishing several food chains [if one accepts the Ediacara fauna as diffusion feeders]. It has also been suggested that deposit feeding began much earlier, within the Riphean more than 1000 Ma ago (Brasier, 1979), but this issue is still unresolved. Damaged trilobite carapaces and the gut contents of priapulid worms in the Early to Mid-Cambrian also provide evidence for larger carnivores (Briggs and Whittington, 1985; Conway Morris and Whittington, 1985) and bored shells for evidence of possible predators or parasites (McMenamin, 1986). This suggests there were second order consumers around to enhance the upper levels of the food chain. Nevertheless there is little evidence that food chains were long and food webs complex in the Cambrian. Macroborers found in Early Cambrian patch reefs of Labrador (James *et al.*, 1977) indicate early utilization of the substrate as a shelter mechanism: not all borers, therefore mark predation. Also, much of the Early Cambrian fauna

appears to have been experimental: many of the earliest skeletal fossils were small in size, aberrant in symmetry or belonged to groups which became extinct by mid-Cambrian time. Thus it was largely a limited success. The reason for failure of the Early Cambrian fauna is unknown: Middle to Late Cambrian and even most Early Ordovician shallow marine faunas are dominated by arthropods, sponges and worm-like invertebrates, with only the first having an excellent skeletal record. The general lack or overall scarcity of shelly and coralline organisms with skeletons for nearly 60 million years (Lenian through Llanvirn time) must have created substrates, and substrate exploitation techniques, different from those seen in the middle and later Paleozoic. Reefs, for example, following the extinction of the archeocyathids, did not reappear until the Caradoc or Middle Ordovician (except for algal stromatolites and rare sponge mounds in the Early Ordovician). These may have been more difficult to establish unless there were more organisms with hard parts around. The fossil record does not, of course, tell us a great deal about the soft-bodied or weakly skeletalized faunas nor about micro-faunas, except under unusual circumstances of preservation, such as represented by the Middle Cambrian Burgess Shale of Canada or the Early Cambrian Buen Formation of north Greenland (Whittington and Conway Morris, 1985; Conway Morris *et al.*, 1987). Such "soft-bodied" ecosystems in deeper waters may have functioned differently from those in

shallow, nearshore habitats.

The major radiation of the Paleozoic fauna and the establishment of rich shelly and coralline shelf communities leading up to patch reef associations did not occur until Middle Ordovician (Llandeilo-Caradoc) time. Why these took nearly 60 million years to become established is unknown: it represents one of the puzzles of Early Paleozoic history. At any rate, the basic pattern of complex marine food chains and food webs, with second and third order consumers, founded in the Middle Ordovician, appears to have remained relatively unchanged in the Phanerozoic. Except for faunal replacement, the addition of some evolutionary morphological novelties, the exploitation of deeper burrowing niches in the Mesozoic, and periodic mass extinctions which left large scale ecosystems relatively empty for periods of 4 to 10 million years, marine shelf habitats appear to have been fairly uniform. The fabric, structure and architecture of coral-sponge reefs of the Devonian, for example, are not that different from those of today. Predation increased with the arrival of shell-breaking placoderm and dipnoan fishes in Devonian seas, and these were replaced by other vertebrate predators in the Carboniferous, and by a larger array of both vertebrate and invertebrate marine predators in the Mesozoic (Vermeij, 1978).

Invasion of the land

In terms of trophic structure, the invasion of the land environment was the next major step. Precisely how and when this occurred is still debated. Cuticular remains and spore tetrads, possibly produced by liverworts and mosses, are known from mid-Ordovician (Caradoc) rocks of Libya (Gray *et al.*, 1982; Edwards *et al.*, 1986). Late Ordovician burrows in soils suggest the existence of sizable organisms such as millipedes, which may have fed on plant litter (Retallack and Feakes, 1987). These presume the development of a primitive soil-based, *detritus-feeding* food chain, perhaps the forerunner of other land ecosystems. Undisputed vascular land plant remains occur in Late Silurian terrestrial sediments: this flora rapidly became uniform and widespread (Edwards, 1980; Edwards and Fanning, 1985). Whether all these earliest plants lived in very wet, peaty soils or in shallow lakes, as might be expected if land plants derived from marine ancestors, is not clear: both thick-walled and thin-walled stems are known, thick walls suggesting adaptations to an erect, self-supporting habit and drier habitats. It has been pointed out that early soils would have had a low nutrient status, lower organic content (Beerbower, 1985), reduced porosity and permeability, and physical instability because of limited plant cover and minor presence (?) of soil recyclers (e.g., protozoans). Rolfe (1980) has suggested that there were no soil nematodes until the Carboniferous. It seems likely, therefore, that the evolution of

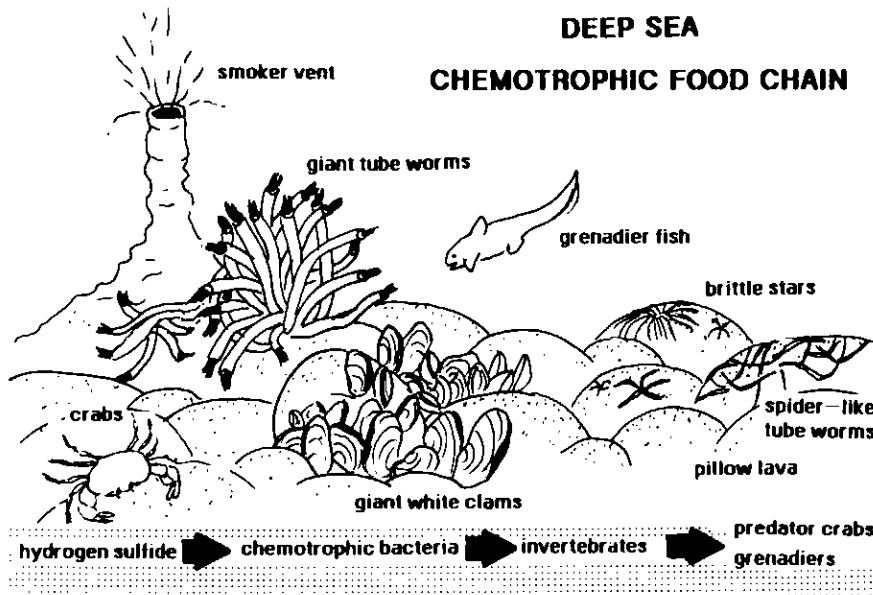


Figure 6 Chemolithotrophic food chain. Modern deep sea vent and passive margin areas with hydrogen sulphide seeps support a unique community which does not rely on solar, but rather chemical, energy. At the base of the food chain are the chemotrophic bacteria, which are consumed by or which live symbiotically within invertebrates around the seeps (e.g., the giant, gutless tube worm *Riftia*). The Late Precambrian, shallow water Ediacaran fauna perhaps had broad similarities in the sense that autotrophic symbionts may have precluded the need for a mouth and digestive tract, e.g., in giant "flatworms" such as *Dickinsonia* and in the "seapen" *Rangia*.

soils is tied in to evolution of fully terrestrial food chains. The presence in the Rhynie Chert of plant-juice sucking insects, plant-digesting myriapods and carnivorous spiders which fed on insects (Rolfe, 1980, 1985), demonstrates that a *plant-based food economy*, at least at the invertebrate level, existed by the Early Devonian.

By the end of the Middle Devonian, fossilized parts of bushy shrubs, small trees and hefty trunks of club-mosses, ferns and progymnosperms suggest heights up to 13 m were reached (Edwards, 1980). This indicates the probability of the growth of forests displaying ecological tiering, conquest of drier environments, development of wind-dispersed seeds and co-evolution of animal life in arboreal tropical ecosystems in the Late Devonian. The evolution of leaves and a fully developed high canopy tree-top ecosystem would have stimulated further advances in a *browsing* food chain for terrestrial invertebrates: insects and spiders evolved explosively in the Carboniferous. Other invertebrates, e.g., bivalves, gastropods and terrestrial polychaetes, and early vertebrates, e.g., amphibians, also served to make the food web more complex at this time. The conquest of terrestrial habitats was by then nearly complete (Padian and Clemens, 1985). The oldest tetrapods, amphibians and reptiles, were probably carnivores, living on arthropods, molluscs, worms or other vertebrates. Tetrapod herbivory was probably not established until the late Carboniferous with the appearance of diadectid and edaphosaur para-mammals (Milner, 1980).

The final phase appears to have been a *reverse conquest of marine environments* by autotrophic groups that originated on land. During the Late Cretaceous and Early Tertiary certain angiosperms, sea grasses and possibly mangroves, successfully invaded the seas, thus providing a supplementary food resource for evolving herbivorous marine vertebrates.

Tiering in ecosystems

Within many ecosystems there are usually marked trends by the immobile or relatively fixed organisms to seek out and compete for specific optimal conditions, mostly in the search for food, space and light. Some do this by rapid upward growth, finding food, light and space near the top; others are adapted to life at the substrate-water interface (see Figure 7). This often results in a strong vertical layering effect which has been called stratification by neontologists (e.g., Odum, 1971), and more recently "*tiering*" by geologists (Ausich and Bottjer, 1982: to avoid confusion with geological, thermal or chemical stratification). Some of the best known examples of tiering have come from tropical rain forests: the initial competition for light in the upper canopy is matched by compartmentalization of cool-adapted plant

species living in the understory. The epiphytic arboreal orchids, for example, can tolerate bright light but live in the shade because optimum growing conditions require cooler temperatures. Insect and bird populations, in turn, occupy different levels within the forest ecosystem. Thus, forests are tiered into an upper autotrophic and lower heterotrophic sequence.

In marine environments, there is a trend for sessile producers to compete for light and for sessile consumers, especially suspension feeders, to compete for food (or both). In very clear seas with little sediment, plankton or detritus in suspension, light can penetrate to 100 or 150 m and algal autotrophs such as seaweeds can reach lengths of 10 to 20 m above the sea floor. The Jurassic Posidonienschiefer of Germany have yielded colonies of the crinoid *Seirocrinus* with stems more than 15 m long (Seilacher *et al.*, 1968), an unusual example of tiering. Kauffmann (1978) noted that these were attached to sunken logs, suggesting that these crinoids were feeding at least 15 m above the substrate. Epifaunal tiering generally occurs at three levels: a very low level at or near the substrate (<5 cm), an intermediate level reached by the larger benthos (5-25 cm), and a high level used by long-stemmed or epifaunally attached organisms (Figure 7). Such tiering is more apparent in shallow marine environments, and may be absent in the deep sea where life is less abundant and benthic competition for light, space and food not so critical. Ausich and Bottjer (1982) concluded that significant epibenthic feeding levels were not developed until the Ordovician. Infaunal

tiering, *i.e.*, tiering down into the substrate, was, however, weak until the evolution of deeper burrowing bivalves and echinoids in the latest Paleozoic. Infaunal tiering appears to be developed, at or near the sediment-water interface (<5 cm deep), deeper down at intermediate levels (5-25 cm) and at substantial depths, e.g., by "super-shrimp" and echinoids (Figure 8). Limits are defined by the capacity of the organism to dig as deep as possible. Burrowers include several feeding categories of organisms: deposit feeders that mine the sediment for food; carnivores, herbivores or deposit feeders that use the burrows merely for shelter, reproduction or food storage and feed on the surface above; or "harvesters" that line the burrows with mucus and grow "crops" of fungi or bacteria which are in turn consumed.

Tiering may also be a factor in hard substrate and reef habitats, though the causes may be more difficult to evaluate. Many hermatypic reef dwellers possess symbiotic zooxanthellae (autotrophic dinoflagellate algae which add colour to the host and stimulate carbonate production). This may therefore induce competition of vertical space as more rapidly growing species search not only for food but also for light. However, water depth on the reef flat is often very limited and aggression to increase lateral space may be more important. Epifaunal tiering is probably more evident, therefore, in water depths of several metres or more, and absent or limited in the intertidal to shallow subtidal reaches of less than 1 m.

In the Early Cambrian, the oldest shelly fossils were very small (<1.2 cm), stalked

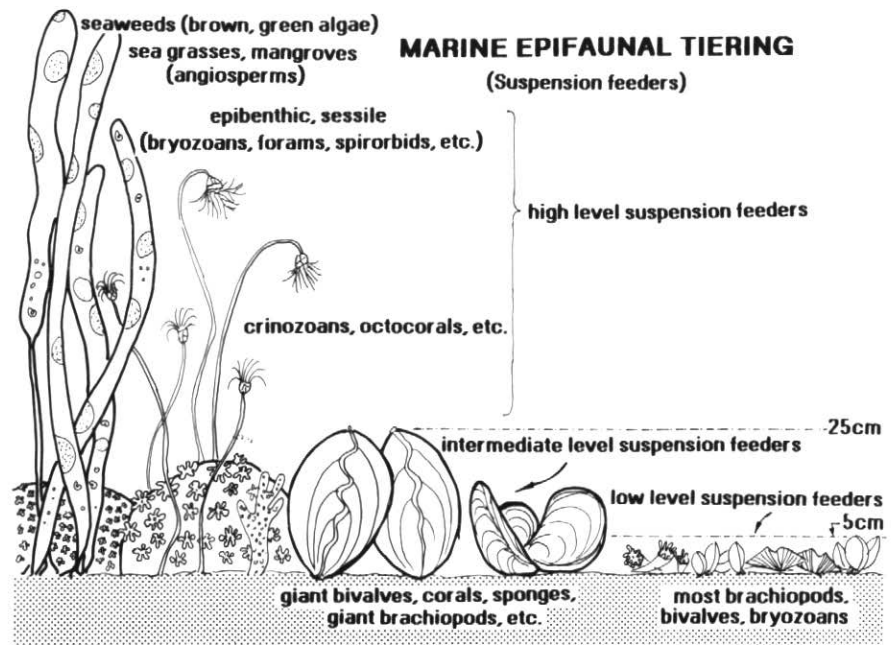


Figure 7 Tiering of epifauna. Organisms which live above the substrate, especially sessile suspension feeders, compete for food and light by catching their nutrients at various levels in the water mass (here arbitrarily set at 5 cm and 25 cm limits). This is similar to light and temperature competition in the tropical rain forest.

animals such as eocrinoids were of limited length (<10 cm tall) and sessile sponges such as the archeocyathids had limited vertical growth capacity and were rarely colonial. Development of a longer crinoid stalk came in the mid-Ordovician and large, cylindrical sponges (e.g., the aulacirid stromatoporoids) more than 3 m high were not present until the late Caradoc and Ashgill (Copper and Grawbarger, 1978). Large colonial tabulate corals more than 50 cm high are known from the Caradoc; large upright solitary rugosans to 30 cm in length and colonial rugosans to 40-50 cm in height did not appear until the Ashgill. Rapid vertical growth may not have been a direct response to light or food availability: a cylindrical or fasciculate (branching or "organ-pipe") architecture may also have been a reflection of a better capacity to shed sediment.

Infaunal tiering also started in the later Ordovician, with the establishment of shallow burrowing bivalves and lingulid brachiopods (Ausich and Bottjer, 1982). Initially this was possibly only related to feeding, as sediments represent a rich food resource that can be mined. In the late Paleozoic, infaunal bivalves diversified and the evolution of the fused siphon marked an explosion of the deeper burrowing niche in the Mesozoic (Stanley, 1970). This was matched by the mid-Mesozoic expansion of infaunal echinoids, shrimps and polychaetes. The rapid development of Mesozoic carnivores (e.g., marine fish and reptiles, starfishes, crabs and boring gastropods that preyed on the benthic fauna) may also have accelerated the use of burrowing as an escape technique, emphasizing infaunal tiering.

Paleocommunities

The terms community and paleo("fossil")-community have had very diverse usage by biologists and paleontologists, although it is clear that the properties recognized, both descriptive and causal, are fairly universal. Communities are the living components of ecosystems. Biologists generally define communities as *species populations which function together as a unit and live in a prescribed area*. Paleontologists have problems defining communities because of time-averaging or condensation (compression of several heterochronous populations into one bed), because of preservational loss (most soft-bodied components, most of the producer biomass and much of the skeletal record may be lost) and because the ecologic structure of the community must usually be interpreted (it can't be seen). As a result, some have favoured the use of terms such as associations or assemblages which are less precise and more objective (Boucot, 1981). Assemblages represent the collected field sample; associations are recognizable distributional patterns in collected assemblages. Some have defined fossil communities in a time or geographic framework, i.e., as *recurring, co-occurring species which are recognizable laterally over wide areas or vertically through time, usually in relation to a specific sedimentary setting*. Paleontologists must at least make an attempt to reconstruct communities of the past so that we can understand their development and evolution.

Communities, as ecologic units, have properties. They have a *spatial framework*, distribution, niche or environmental setting (e.g., a "reef" community, an intertidal community). They have *structure* and *hierarchy*

("pecking" orders, often related to feeding and spatial relationships within the community). They are *dynamic* having short term pathways of energy, reproduction, change, succession, etc.). They have *diversity* and *density* (i.e., biomass: there is no community of a single individual or species). And, they *change through time* (evolution, replacement, extinction: see Jablonski *et al.*, 1983; Sheehan, 1985). Not all of these properties are necessarily determinable or recognizable in the fossil record, but approximations may be made by detailed and careful analysis of the functional morphology of organisms, population counts, knowledge of species inter-relationships and taphonomic studies. To be definable as a paleo-community, the assemblages should normally occur over a relatively wide area and recur repeatedly through a time frame. A single community defined in a single locality at one horizon is of little comparative value in geology, though it may be of unique interest.

Communities are usually named after their *location* (e.g., estuarine community, rainforest community), a *dominant, prominent* or *indicator species* (e.g., the *Eccoelia* community in the Early Silurian: Ziegler, 1965) or a *functional attribute* (benthic community, suspension feeding community). Community boundaries are rarely sharp, usually gradational. The term *ecotone* or *ecocline* has been used for a gradational, synchronous lateral change, i.e., a gradient between adjacent communities. Stratigraphic community correlation or *coenocorrelation* is an attempt to relate coeval communities across ecological boundary lines and gradients, usually in onshore to offshore transects (for Ordovician examples see Cisne and Rabe, 1978). The purpose of this has been to determine shifts of communities through time, e.g., as a reflection of basin, climatic or sea level change. *Biomass* (weight of shell and extrapolated soft parts) may be used as a measure of fossil community structure and development, at least for the Cenozoic, since it represents the net amount of new organic matter produced by the organisms when alive (Staff *et al.*, 1985). This method is more accurate than individual abundance figures calculated from species counts, and ratios between living communities and their potential death assemblages.

Ecological succession in communities or in the ecosystem is the relatively predictable, dynamic maturation and development of associated species in specific habitats leading toward increasing biological control of the environment and an equilibrium, stabilized ecosystem (Odum, 1969). Beginning *pioneer* (or *developmental*) and end-point *climax* (or *mature*) phases of a succession may be recognized, each phase being characterized by wide-ranging species and community level interactions. Odum (1971) later identified *autogenic* (biotic) processes and *allogenic* (physical/chemical) processes that

MARINE INFAUNAL TIERING

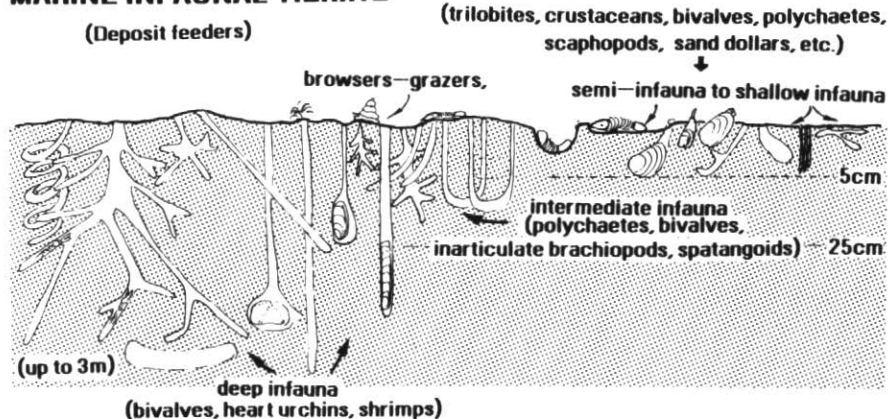


Figure 8 Infaunal tiering. During the Phanerozoic there was increasing utilization of the substrate for food and shelter. "Superburrowers" (deep infauna) were scarce until the Mesozoic; shallow burrowing was dominant in the Paleozoic. Increasing predation pressure from the arrival of carnivorous Mesozoic starfish, crabs, gastropods, fish, reptiles and birds, may have selectively forced this deeper burrowing. Such increased bioturbation also had drastic impacts on sedimentary regimes: more fine sediment was put into suspension, bedding planes were heavily disturbed and submarine erosion and sediment transport became more prevalent.

acted on the system, but these are often difficult to identify in fossil assemblages. The term *seré* refers to a sequence of communities replacing one another as they become established to reach an equilibrium over time [this term is almost synonymous with succession].

Ecological succession was applied to paleontology with the work of Walker and Alberstadt (1975), who defined four stages of succession in benthic communities (stabilization, colonization, diversification and domination). However, the first two refer to developmental stages, and the "domination" stage is simply the organized phase of diversification where zoning of community elements is very strong; thus diversification and domination both represent the climax. Where allogenic controls are very strong, no real ecological succession may result, simply the presence of stressed, replaced communities induced by migration, transgression or regression, change in sediment supply, climatic change, etc. into a habitat. This has led some to identify true successions only as those which are autogenic (Rollins *et al.*, 1979; McCall and Tevesz, 1983). Change is also an inherent part of most communities and ecosystems. It was long assumed that increased diversity in ecological succession brought stability and equilibrium with it [stability of population is now called *constancy* and if the number of species stays the same this is called *persistence*: Lewin, 1986]. However, the whole community fluctuates in the long term about a mean, perhaps to some extent driven by external perturbations. Thus, counterintuitively, short term change is often needed to maintain long-term persistence and constancy in diversity and populations (Lewin, 1986). All communities are ultimately controlled by the environment surrounding them (otherwise we would find reefs growing on mountain tops!), but within communities there are strong interactions which lead to internal controls. These are difficult to assess: autogenic successions, in that sense, are the only real ecological successions. However, it should be kept in mind that the early stages of succession have stronger allogenic controls than the later and thus a range of variation in controls is inevitable.

Species (population) interactions

Communities are composed of populations of species. Most communities also experience a temporal balance or *equilibrium* (often called homeostasis) at which the species within the community reach a dynamic fluctuation around a mean in terms of their growth, density and relative dominance of the volume or substrate occupied. This suggests that there is normally interaction between species that live together. Some have even gone so far as to suggest that all such interactions should be called *symbiosis* (covering positive, negative and neutral

association: see Odum, 1972), though this is more usually restricted to relationships where one or both partners benefit directly, and live on or within the other (e.g., commensalism, mutualism). Though ostensibly community ecology seeks to determine patterns and processes, and to generalize from them, determination of relationships is far from simple in both living and ancient communities and especially difficult in the latter. What are some of the relationships?

In general, there are three types of interactions: *neutral*, *positive* (beneficial to one or both) or *negative* (inhibitory). Sometimes a rider is attached to those relationships: an obligatory relationship is one in which the two partners cannot live without each other or do so only rarely, and a non-obligatory one is where the two can be found together but can also survive apart or with other species. *Neutralism* defines a relationship where species co-occur but do not affect each other. *Commensalism* is a positive relationship where the commensal benefits without damage to the host or partner. *Mutualism* is an interaction favourable to both species (sometimes proto-co-operation has been used to distinguish non-obligate partners). *Competition* defines relationships in which there is direct inhibition of each species for resources or space. In *amensalism* one species is inhibited, but not the other. *Predation* defines the predator-prey feeding relationship. *Parasitism* is a relationship in which the parasite lives off the "interest" and sometimes the "capital" of the host (effective parasites will rarely extinguish species). Many of these interactions are almost impossible to determine in the fossil record and depend on inference, co-occurrence and analysis of morphology. For example, the mutualistic symbiosis of modern hermatypic scleractinian corals and algal zooxanthellae may or may not have been present in their Paleozoic equivalents, the rugose and tabulate corals (Cowen, 1983). On the one hand, larger corallite size has been used to infer fossil zooxanthellate symbiosis (Page *et al.*, 1984) and, on the other, small polyp and corallite sizes has been identified as characteristic of zooxanthellate symbiosis (Coates and Oliver, 1986).

Community interactions play an important role in natural selection and evolution. Some of these interactions may co-evolve (Futuyama and Slatkin, 1983). Competition is perhaps one of the most controversial relationships and its importance has recently been questioned (Lewin, 1983). Clearly, competition for food, resources, space and reproduction does exist, but what is its role and how is it measurable? In the framework of Darwinian natural selection, how many species can a community support? Moreover, how many related species with similar ecological requirements can co-exist (*i.e.*, in guilds, a guild being a group of different organisms with more or less the same eco-

logical demands on the habitat)? Are habitat differences, climate, random events (hurricanes, wildfires), immigration and predation more important? Are vertical (herbivore-carnivore) interactions in the food chain more significant than horizontal competition? In general, it has been assumed that if a resource is limited, organisms will compete for it, and that no two species with identical niche requirements can co-exist (one will win out: Gause's Principle). Following from this, it has been concluded that there must be enough of a difference between competing species to enable each to carve out its own niche, e.g., in terms of growth (rates, size, shape, technique), larval settlement preference (time, space, nature of substrate), feeding mechanisms and mobility (see Jackson, 1983). Some of these differences are difficult to evaluate even in living organisms; they can only be suggested by inference for fossils. In plants, competition appears to be much more important than in animals because, within communities, plants are similar in their physical-chemical and metabolic needs and are not separated into trophic guilds. There is some evidence for this in the successive radiations and replacements of plant groups through time because plant groups commonly cross extinction boundaries (Niklas *et al.*, 1985).

Modes of life

Among modes of life, or behavioural patterns, that can be analyzed in the fossil record, usually two stand out: feeding and mobility (the latter has little significance for sessile organisms who await their food). Feeding will be considered first. Food resources are variable and may consist of dissolved and colloidal organic molecules, organic rich sediment, organic detritus, and live or dead plants and animals. These are selected for usable, specific nutrients and size. For benthic communities, a useful classification of feeding types was elaborated by Walker and Bambach (1974). They recognized six dominant feeding types in marine substrate habitats: suspension and deposit feeders, browsers, carnivores, scavengers and parasites, and sorted these into subgroups based on epifaunal or infaunal occurrence. Many other subgroups may be recognized within individual phyla. Recognition of feeding types is essential in the reconstruction of communities and their food chains.

Mobility is also a variable factor. Plants are essentially immobile unless they float, but seeds, fruits, pollen and spores may be widely dispersed by wind, water or organisms (similar dispersion patterns exist for monerans and protoctists). Mobility is more critical for invertebrates and essential for vertebrates. A number of phyla are nearly exclusively *sessile*, *i.e.*, in adult stages the animals are fixed or fused to the substrate (see the sponges, corals, bryozoans, and brachiopods). This fixation is by cementation

to hard objects, or by development of special holdfasts, stalks or membranes. A *sedentary* mode of life refers to organisms which rest on the substrate; quite commonly these have special adaptations to hard, sandy or soft muddy substrates in the form of frills, spines, flattened or splayed out morphology (to prevent sinking) or temporary anchors. We see this in many brachiopods, bivalves and some echinoderms. *Actively mobile* (or *vagile*) marine organisms include those which crawl or creep on or within the substrate (e.g., trilobites, gastropods, echinozoans) and those that move in the water-mass, such as the swimming cephalopods, fish, pectinid bivalves. A number of organisms are *passively mobile*: they do this by attaching to plankton or swimming or crawling nekton and benthos. Terrestrial vertebrates are even more versatile in their mobility. These include runners, jumpers, crawlers, creepers, climbers, diggers, fliers, gliders, etc. Mechanisms for both feeding and mobility are highly specialized even within groups: the study of *functional morphology* is largely concerned with these two aspects. It is an invaluable component of paleoecology.

Summary

Geologists are coming to realize that many small scale processes, like the daily life habits of common organisms, have a global and long term impact on the planet. Biological processes have had an enormous effect on the Earth's atmosphere, oceans and land surfaces. The evolution of life is directly linked with major changes and fluctuations in geological processes through time. Mass extinctions, whether caused internally by climatic disruptions or externally by extraterrestrial impacts, have periodically reset the clock of biological change and forced the biosphere into new directions. These changes, and the processes which produced them, are not yet fully understood. It is the task of paleoecology to understand how these processes worked in the past and to develop models that will help us to predict future change.

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