Origins, Evolution, and Diversification of Zooplankton

Susan Rigby[1] and Clare V. Milsom[2]
[1]Department of Geology and Geophysics, University of Edinburgh, Edinburgh EH9 3JW, United Kingdom; e-mail: suerigby@glg.ed.ac.uk; [2]School of Biological and Earth Sciences, Liverpool John Moores University, Liverpool L3 3AF, United Kingdom; e-mail: BECSMILS@livjm.ac.uk

■ **Abstract**   Fossil plankton are difficult to identify but have formed a major component of most marine ecosystems throughout geological time. The earliest fossil heterotrophs include planktic forms, and subsequent adaptive innovations quickly appeared in the plankton; these include metazoans and animals with hard parts. Movement into the plankton occurred sporadically throughout geological history and seems to have been independent of any biological or environmental forcing mechanism. Subsequent radiations and extinctions in the cohort of plankton closely reflect events in the benthos. The diversity of zooplankton rose quickly during the early Paleozoic era, but low plankton diversity characterized the late Paleozoic. Significant radiations during early Mesozoic times led to an overall increase in diversity through the Phanerozoic eon. As the composition of the zooplankton has changed, so has their effect on biogeochemical cycles.

INTRODUCTION

In this paper, we review the origins of the major modern groups of zooplankton and of extinct groups that have been geologically significant. To accomplish this, we review the ways in which fossil plankton have been identified and defined. We review the likely controls on the zooplankton over geological time and discuss the pattern of origination and evolution of planktic organisms. Finally, we consider the biogeochemical implications of this evolutionary history. The approach is chronological, moving from the Proterozoic era to recent time. Previous reviews have partially covered the Holocene and include discussions of the Paleozoic plankton of North America (92), early Paleozoic plankton in general (13), the origin and early evolution of the planktic system (102), and the origins and evolution of microplankton (62, 115).

Members of the zooplankton have the widest geographical spread and greatest numerical abundance of any animals. Modern zooplankton are important

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contributors to global biomass and to the chemistry of the oceans, a dominant means of flux to the seabed (76), and a source of food for many large animals. The microzooplankton are dominated by flagellate protists, including some dinoflagellates and zooflagellates, and by amoebae such as foraminifera and radiolarians. Planktic ciliates are common, although the major group of these, the tintinnids, have proteinaceous tests and leave little record in the sediment (59). The macrozooplankton include a wide range of solitary and colonial cnidarians, chaetognath and polychaete worms, and holoplanktic gastropods. Crustaceans are among the most common macrozooplankton, with copepods, euphausiids, amphipods, ostracodes, and decapods all abundant and diverse (83). Urochordates are widespread with two planktic groups, appendicularians and salps. Larval stages of invertebrates and fish make up a significant proportion of the heterotrophic plankton in the modern ocean, remaining as part of the plankton for periods ranging from minutes to years.

Preservation of plankton in the fossil record is generally poor because of postmortem transport and because morphological adaptations, particularly the reduction of skeletal material, reduce the fossilization potential of plankton. The characterization of fossil plankton is also rather different from that of modern zooplankton, and this has led to an historical bias against including organisms with a limited swimming capacity in this classification.

The zooplankton form a cohort of organisms that are unusually dependent on the physical environment surrounding them. They are supported, transported, and fed by the surrounding water. The degree to which intra- or interspecific competition occurs in this environment is partly dictated by chance encounters, and, as a result, it appears that very similar species are able to coexist indefinitely (43). This long-term coexistence of species that might be expected to compete is known as the paradox of the plankton (43). Because of the likely dominance of abiotic over biotic controls and the weak interspecific competition that is characteristic of the plankton, it has been possible for organisms to migrate into this environment over a prolonged period (88). A phylogenetic analysis of the zooplankton shows that high-level clades of organisms have colonized this realm from the benthos rather than evolving in situ (88). Such colonization has occurred throughout geological time, contrasting strongly with the patterns of colonization seen, for example, on land (29, 87).

In an analysis of ecosystem evolution, Vermeij suggested (121, p. xii) that organisms, including predators, have become better adapted through time, making many environments "riskier places in which to live." The long geological history of migration into the planktic realm suggests that this theory is not applicable to the zooplankton. Kinetic models of evolutionary change and diversification based on analogy with the logistic equation suggest that an ecosystem will experience early and rapid diversification of organisms, followed by a slower increase as organisms begin to compete actively (100). The planktic ecosystem likewise seems to be an exception to this model.

IDENTIFYING FOSSIL PLANKTON

Analysis of open-ocean fossil ecosystems has been impeded by a lack of consensus regarding the actual organisms that inhabited this regime. Two problems of definition exist. The first is that some authors have failed to distinguish between a pelagic position and a planktic life habit. Thus a suggested criterion for the definition of planktic organisms was their "...wide distribution, their lack of ecological connection with any exclusive sedimentary environment, and their predominance in sediments representing de-oxygenated bottom conditions" (13, p. 456). This definition is actually of pelagic rather than planktic organisms, because it defines a spatial position in the water column rather than a mode of life.

The second problem is that the definition of fossil plankton, as used by palaeontologists, has been much more rigid and prescriptive than that used by modern plankton specialists. The modern definition of planktic habit is that the organisms concerned must be unable to move against prevailing currents (83). However, the majority of modern planktic organisms are active swimmers, moving vertically by hundreds of meters each day. They can also be large, with siphonophores reaching lengths of 10 m, giant salps exceeding 1 m, and bathypelagic euphausiids attaining lengths of 10 cm. Members of the plankton, such as many planktic gastropods, can be active predators (58). In the modern oceans, all pelagic invertebrates are considered planktic, with the exception of some species of squid (83). However, in case studies of fossils, organisms that could move are generally excluded from the plankton, and only those with no apparent means of locomotion, such as graptolites, have been defined as planktic in habit. Organisms that appear to have been adapted for active swimming are defined as pelagic (35) or even as nektonic (RJ Aldridge, personal communication). A sensible solution to this problem would be to regard all fossilized pelagic invertebrates, apart from cephalopods, as part of the plankton in a broad sense, because this would bring fossil analyses into parity with the definitions applied to modern systems.

Recent studies of planktic life habit have tended to be organism specific, and a definitive list of criteria used to define such an ecology has not been established. Ruedemann (92) proposed that faunal association was fundamental in determining a planktic mode of life, and Fortey (35) established three lines of evidence that, he argued, should be applied in any attempt to deduce mode of life: arguments from analogy, arguments based on suitability of design, and the use of independent geological evidence. Discussed below are morphological and sedimentological factors that are considered indicative of a pelagic and/or planktic mode of life. In fact, most of these factors apply to the determination of location rather than life habit.

Defining a Pelagic Position

Rudemann (92) stated that any Paleozoic fauna associated with graptolites must be planktic, unless it also occurred with obviously benthic forms. Two problems

with a more general application of this method are that plankton do occur with obviously benthic faunas and that a determinant group, such as graptolites, may have its life habit misdiagnosed. A potential circularity is inherent in any argument that identifies one species' mode of life from that inferred for another. Above all, the result of such an analysis is a determinant for living position and not for life habit, and it can therefore contribute to the inference that an organism was pelagic, but can say nothing meaningful about its planktic or nektonic lifestyle.

Organisms with a widespread and transoceanic distribution are usually assumed to have been pelagic (37, 103), with the obvious exception of individuals that drift for long distances postmortem. Facies has been cited as a critical indicator of a planktic mode of life (92). The occurrence of Ordovician inarticulate brachiopods in black shales has led to the conclusion that they were pelagic (92, 96). However, arguments based on facies distribution have also been used to suggest that most inarticulate brachiopods did not have holopelagic lifestyles (46). As with faunal relationships, fossil distribution is informative with regard to life position rather than habit.

Defining a Planktic Habit

A single feature of a fossil that seems to have a modern analog in a planktic organism allows the design of the rest of the fossil to be assessed for suitability for a planktic habit (37). Ruedemann (92) listed the morphological characteristics of plankton as small size and thin, chitinous shells. These characteristics have been used to determine a planktic life habit for the bivalves *Bositra radiata parva* and *Bositra radiata magna* (77), but they have also been used to support suggestions of a benthic mode of life for these organisms (52, 53).

Modern plankton are characterized by reduced skeletons, gas or fat bodies that reduce their overall density, flattened forms, and the frequent presence of spines or other features that increase drag. These adaptations might be used as good markers to determine a planktic habit in fossils.

Bulman (13) demonstrated, from an assessment of the functional morphology of the nema, that graptolites were probably holoplanktic rather than epiplanktic on seaweed. Analysis of the gross morphology of graptolites and of their "design" (see 37) shows that they were hydrodynamically stable and possessed modifications of form that would have enhanced their efficiency in a truly planktic mode of life (85, 89).

A strong argument for a planktic habit can be made if close living relatives of the group share this habit. It can surely be accepted that most single-celled organisms with a broad geographical distribution were planktic if this is the case for their living relatives. This argument applies, for example, to radiolaria and coccolithophorids. It also applies to foraminifera, despite the multiple evolution of planktic from benthic forms (26). Clearly, this is the strongest single line of

evidence for mode of life. However, its applicability declines when older fossils, which are increasingly less likely to have living relatives, are considered.

TEMPORARY MEMBERS OF THE ZOOPLANKTON: Pseudoplankton and Planktotrophic Larvae

Within the zooplankton there is a long evolutionary history of facultative or obligate pseudoplankton and of organisms with a planktic larval stage of long duration. The constraints on these groups are substantially different from those of the true plankton, but their persistence in the planktic realm makes their contribution important.

Pseudoplanktic organisms are difficult to distinguish from deep-water-benthos and from transported elements of fossilized faunal assemblages. This is particularly true of facultative elements of the pseudoplankton present coevally in benthic settings. One criterion to distinguish a floating life from a benthic one is rarity—the argument is that floating substrates are rare and so should their colonizers be (126). Pseudoplankton are also identified by their distribution across a wide variety of substrates and with a wide geographical distribution. Uncertainty remains in the identification of possible in vivo colonization while the substrate was floating, as opposed to postmortem colonization on the seabed. Some specimens of epiplankton have been found overgrown by their host (71) or orientated toward a possible source of food at the aperture of a cephalopod (98), but in many cases convincing arguments cannot be made for either the locale of colonization (cf the arguments of 53 and 98) or the health of the substrate organism.

Pseudoplankton diversity appears to have been variable through the Phanerozoic eon, controlled largely by the availability of appropriate floating substrates. The first pseudoplankton appear to have been Ordovician inarticulate brachiopods and bryozoans, some of which are host specific, implying an obligate pseudoplanktic lifestyle (4). High pseudoplankton diversity in the Ordovician and Devonian periods is attributed to the abundance of large orthoconic nautiloids and driftwood, respectively, but no simple correlation explains diversity peaks in the Permian and Cretaceous periods (126).

Few members of the obligate pseudoplankton have a good fossil record. When a fossil record is known and evolutionary lineages can be traced, it appears that pseudoplankton evolve repeatedly from benthic ancestors rather than from one another (126).

The other common, temporary constituents of the zooplankton are the larval stages of benthic invertebrates and nektonic vertebrates. It has been suggested that possession of a planktic larval stage is the primitive metazoan condition (49), although this is disputed (33, 110). It is likely that the majority of benthic invertebrate species have planktic larvae (118). Certain groups may tend to evolve

away from this strategy (80), possibly because of the likelihood of dispersal into unfavorable habitats and the high energetic cost of metamorphosis. Jablonski (48) suggested that there is a link between oceanic conditions and the evolution of planktotrophic, planktic larvae, as exemplified by the evolutionary history of neogastropods. This group originated during the Cretaceous period, at a time of high sea levels and broad geographical habitats, when planktic larvae had the advantage of suitable settlement sites at a distance from their point of origin. As climatic conditions became more heterogeneous, nonplanktotrophic or nonplanktic strategies were favored, because suitable sites would most likely have been encountered close to the site of spawning (48). If this explanation is generally valid, there should be a broad correlation between periods of climatic homogeneity and times of common planktotrophic planktic larvae. However, the fossil record of larvae is inadequate to quantify this relationship at present.

MULTIPLE ORIGINS OF ZOOPLANKTON

Nineteen major groups of zooplankton can be demonstrated to have had a benthic origin, either through their fossil record or from their phylogenetic trees (88; Figure 1). Plankton recruitment is achieved by one of three methods: (*a*) adopting a pseudoplanktic strategy, (*b*) paedomorphosis, or (*c*) the migration of mature individuals. The pseudoplanktic route requires the development of a sustainable method of attachment and, in common with paedomorphosis, the possession of a planktic larval stage. Because eggs and larvae have been present in the plankton since the origin of metazoans, neoteny may be considered as a long established route into the plankton.

Absence of a planktic larval stage does not preclude recruitment into the zooplankton. The benthic-to-planktic transition may be possible at a later stage of ontogeny by mature individuals with planktic preadaptations. Thus, Silurian ostracodes adopted a planktic lifestyle by virtue of their enhanced swimming capabilities (103) and thecosome gastropods through the finlike adaptation of their muscular foot (49, 58).

THE EVOLUTIONARY HISTORY OF HOLOZOOPLANKTON

Precambrian Era

The first metazoan zooplankton were probably jellyfish, but their age and detailed taxonomic affinities are disputed. The occurrence of pre-Ediacaran metazoans, said to include ancestral planktic cnidarians, is recorded from India (97). These faunas contain fossils interpreted as large medusae and are suggested to have formed part of an extensive and diverse zooplankton community. They are found
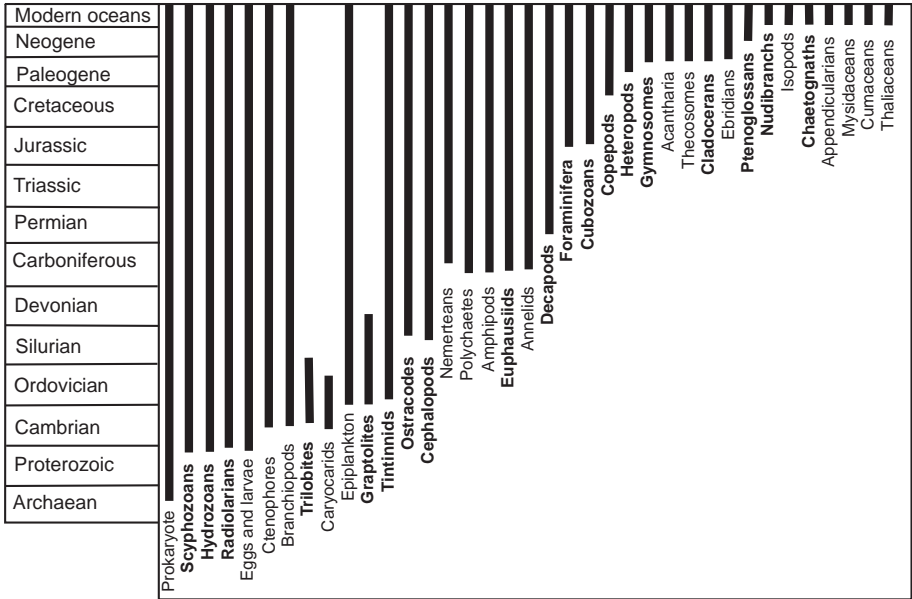
Figure 1 The pattern of origination of zooplankton through the Phanerozoic eon. *Bold type* indicates groups with a known ancestry in the benthos.

in rocks dated at between 900 and 1000 MYA and arguably represent the oldest metazoan fossils to date.

It is more generally agreed that the first medusoid cnidarians belonged to the Ediacaran fauna (44, 123, 124), which appeared around 565 MYA. The lifestyle and taxonomy of Ediacaran fauna have received much attention. If they were metazoans rather than vendobionts (99) or lichens (84), it seems likely that at least some were planktic; some medusiforms have been reinterpreted as benthic organisms (50), but others, notably *Ovatoscutum* and *Rugoconites*, remain as probable plankters. More precise taxonomy is problematic, although Runnegar & Fedonkin (93) were confident of the presence of three genera of Cyclomedusidae and four hydrozoans within the Ediacaran biota.

Experiments conducted on the preservation potential of modern jellyfish suggest it is unsafe to attempt a detailed taxonomic comparison of these Precambrian sand molds and modern taxa (76). However, Norris (76) considered it likely that broad similarities in form between Ediacaran radial fossils and extant jellyfish are a product of evolutionary convergence (76). Evolutionary convergence tends to imply functional convergence, making it likely that, even if their phylogeny is distinct from that of modern jellyfish, the Ediacaran radial fossils were probably planktic.

Second candidates for the earliest metazoan members of the zooplankton are the organisms that appear to have deposited fecal pellets in anoxic shales up to

1900 MYA (90). If these are real fossils rather than artifacts, as the authors convincingly argue (90), then planktic gut-bearing animals might be much older than previously thought. Research on molecular sequence divergence shows a likely point of origin for coelomate organisms in the early Proterozoic era (12, 129) rather than close to the Precambrian-Cambrian boundary (31). However, these molecular results are disputed (3, 24), and a consensus as to the timing of metazoan origins is still lacking.

The other zooplankton group that appears to have been represented in the late Precambrian is the chitinozoans, vase-shaped fossils of ambiguous affinity (47) of possibly the remains of heterotrophic protists or of metazoan eggs. Precambrian fossils of this form have been recovered from Arizona (8) and from Sweden (56). Planktic and planktotrophic larvae must have been present as temporary elements of the zooplankton from the time when metazoans first appeared, sometime during the Proterozoic era, within the envelope of 1500–600 MYA (12, 129). Finally, in considering early growth stages of the Precambrian zooplankton, it is possible that some of the fossils identified as acritarchs and interpreted as autotrophic eukaryotes were actually egg cases (119), although, until more analysis has been done, it is impossible to quantify this.

Cambrian Period

During the early Cambrian period, phytoplankton diversity rose rapidly (122). This may have coincided with the beginning of regular migration of metazoan benthos into the plankton, perhaps as a response to increased grazing pressures on the seabed (14). It is possible that the build-up of zooplankton during the early Cambrian reduced net carbon export from the water column and dampened the magnitude of boom and bust cycles seen in Precambrian phytoplankton (16). The composition of the Cambrian zooplankton was a mixture of Precambrian survivors, such as medusoids and chitinozoans, and new migrants from the benthos, predominantly representatives of newly skeletonized clades of coelomate metazoans. Single-celled animals also migrated into the plankton during the Cambrian period, most importantly radiolarians (62, 74, 81).

Various Cambrian medusoids have been identified (27). Most of these are chondrophores, and several, including *Gelenoptron tentaculum* and *Kullingia delicata*, seem to be Ediacaran survivors (23, 73). Early Cambrian rocks of Canada yield the filtering apparatus of a branchiopod-like crustacean likely to have been planktic for at least part of its life cycle (15). As reconstructed, these crustaceans would have been ≤10 mm long, and the regularity of their filtering nets suggests a planktic source of food. Agnostid trilobites, which reached a diversity peak in the mid- to late Cambrian period, may have been planktic, although some species were probably nektobenthic (72). Other trilobites may have also been pelagic: the early Cambrian genus *Kootenia* is cosmopolitan in distribution, whereas morphological considerations have led to the suggestion of a pelagic habit for *Irvingella* (late Cambrian) and *Centropleura* (mid-Cambrian)

(37). Some of these arthropods were filter feeders, but others were probably predatory (36).

The Cambrian plankton are best recorded in fossil *konservat-lägerstatten*, such as the Chengjiang fauna and the Burgess Shale, which provide a window onto the soft-bodied and lightly skeletonized elements of the Cambrian fauna. Medusi-form metazoans are common on certain bedding planes within the lower Cambrian Chengjiang fauna (20) and are assumed to have had a planktic mode of life. How-ever, putative gut traces within the body cavity mean that these may not have been true cnidarians. Two species of chondrophore are also known from this locality, as are two possible scyphozoans whose taxonomic affinity is less certain (111).

Although undisputed planktic forms compose <0.17% of the Burgess Shale in terms of numbers of individuals (excluding the problematic organism *Eldonia*), they account for ≥7% of the genera present (based on data from 11, 22). This assemblage begins to approach the degree of diversity seen in modern plankton communities and may contain five of the eight major phyla of modern macrozoo-plankton (although the taxonomic affinities of these organisms are often disputed). This high diversity indicates that, at least by middle Cambrian times, the Cambrian radiation had reached the pelagic realm.

The rise in benthic metazoan diversity must also have led to an increase in the abundance and diversity of planktotrophic larvae. If planktotrophy is a primitive larval state (49), it might be expected that the diversity of larvae in the zooplank-ton would have been higher than it is today, although this inference is disputed (102). Fossil evidence of planktic larval stages is sparse, but such an early life stage is predicted from fossil evidence for some Cambrian hyolithids (28) and for actrotretide brachiopods (7, 91).

In summary, it appears that zooplankton diversity rose slightly later than benthic metazoan diversity, possibly in the late Cambrian (102) but more likely in the earlier Cambrian period (16). However, the evolution of the two systems was connected by a variety of feedback mechanisms associated with primary production and transport of material to the seafloor (16, 63, 102). It is even possible that a top-down effect precipitated by the origin of mesozooplankton facilitated the Cambrian radiation itself (16). At present the fossil record and our capacity to model the effects of changes in biota are too poor to clarify what was happening in detail over this critical period in Earth history.

Ordovician and Silurian Periods

Zooplankton continued to migrate into the pelagic realm throughout the late Cambrian and early Ordovician periods, with radiolarians becoming dominant components of the Ordovician microzooplankton (115). Their distribution and changes in their evolutionary rate correlate well with similar changes in macrozoo-plankton (74). Tintinnids appeared in the Ordovician but were rare (21). Chitino-zoa are diverse in rocks of this age (78). The most significant new zooplankton were probably the graptoloids, which originated by neoteny from benthic graptolites

at the beginning of the Ordovician period (37). These colonial hemichordates radiated quickly into a wide variety of shapes, and presumably of niches (86). Trilobites with a likely pelagic habit include *Opipeuter*, *Carolinites*, *Girvanopyge*, *Selenopeltis*, the Bohemillidae, and the cyclopygids (35). These organisms probably radiated into a range of trophic niches and into different parts of the water column (39). Other arthropods also appeared in the plankton. Caryocarids were common elements of the Ordovician and Silurian plankton (92, 109), and ostracodes migrated into the planktic habitat in the Silurian period (103). The full complement of Lower Paleozoic plankton probably included at least one species of inarticulate brachiopod (82). This may have been an epipelagic form, and epiplankton thrived during the Ordovician and Silurian periods, due to the abundance of suitable floating substrates, including the shells of large orthoconic nautiloids (42).

Signor & Vermeij (102) observed that the rise in planktic diversity among metazoans parallels the rise of the Paleozoic fauna documented by Sepkoski (101). They suggested that the cause of this increase in planktic diversity may have been the use of the plankton as a refuge from bioturbation and predation on the seafloor, but this is disputed (120). Martin (68) suggested that the Lower Paleozoic era was a time of superoligotrophy, which limited planktic diversity. However, this assessment was based primarily on microfossil data, and we feel that this apparently low diversity is an artifact caused by the dominance of macrozooplankton over microzooplankton at this time. Although the Lower Paleozoic was generally a time of at least moderate plankton diversity, there is evidence for a major extinction within this realm at the end of the Ordovician period. Sequences of this age in central Nevada show that this extinction affected inshore plankton and graptolites first, extending later to offshore graptolites and to chitinozoans and radiolarians (34).

Devonian to Permian Periods

In the early Devonian period, a noticeable change in faunal composition occurred that correlates approximately with the time at which planktic graptoloids became extinct and with the appearance of ammonoids (57, 74). These changes in the planktic cohort at a relatively high trophic level may have contributed to changes in the system as a whole. In contrast to the previous periods, the Upper Paleozoic was a time of low plankton diversity and muted primary productivity. Late Devonian extinctions particularly affected the plankton and the system was unable to recover until the Jurassic period. This appears to be an unusual and rather protracted extinction event, precipitated by a catastrophic fall in origination rate rather than by a rise in rates of extinction (69).

The long period of impeded plankton development in the late Paleozoic era is a puzzle. The major radiation among vascular land plants and the formation of the first forests in the Devonian period have led various authors to suggest a causal link between vascular plant radiation and the crisis within the plankton. It

has been suggested that the spread of vascular plants caused carbon, nitrogen, and phosphorus to be progressively retained on land (113). As existing marine nutrients were gradually lost into deep-sea sediments, a major biotic crisis was precipitated. An alternative view is that the development of land ecosystems over this period led to increased nutrient runoff and with it increased primary productivity (5). Another hypothesis is that the evolution of increased root masses altered patterns of soil formation, which led to transient pulses of nutrients entering the marine realm and stimulating eutrophication of epicontinental seaways (1). It is possible that prolonged disequilibrium in terrestrial systems may have contributed to the problem, or even that an unpreserved but diverse form of primary plankton producer was present (5), although the latter suggestion seems improbable.

However, even during this crisis in the plankton, old groups of zooplankton persisted. Jellyfish are found throughout the Upper Paleozoic, sometimes in great abundance (107). Over 6000 specimens of soft-bodied cnidarians are reported (40) from the Essex fauna, the marine portion of the Mazon Creek lagerstätte, and these include representatives of all the modern planktic scyphozoan orders. It is likely that new recruits also appeared in the zooplankton during this time of low productivity (88). The oldest pelagic nemertean worms are found in the Mazon Creek fauna (51), and the Carboniferous Granton Shrimp Bed contains the first planktic tomopterid polychaete, *Eotomopteris aldridgei* (9, 11). Carboniferous aeschronectid crustaceans were pelagic (95) as was *Waterstonella*, the most common Granton crustacean (94).

Mesozoic Era

The Mesozoic era saw a massive radiation of microzooplankton and probably also of macrozooplankton. Innovation of skeletal types, particularly the origination of calcareous microplankton, had far-reaching implications throughout the water column. Because the radiation included taxa with siliceous and calcareous skeletons and unmineralized groups, a change in oceanic chemistry is unlikely to have driven the diversification (55). It is postulated that strengthened circulation and increased upwelling may have been generated by continental break-up (55) or that the rise of bioturbating benthic animals may have resulted in more nutrients being recycled back into the water from earlier benthic systems.

Planktic foraminifera evolved first in the Middle Jurassic and were initially meroplanktic, evolving a holoplanktic mode of life in the Hauterivian (25). Radiation patterns within planktic foraminifera can be related to changes in sea level. High sea levels were associated with warmer climates and resulted in more sluggish circulation and increased water column stratification. This resulted in increased species numbers, the development of complex communities, and intense depth specificity of species. Lower sea levels were associated with cooler periods when ocean waters were well mixed. This led to decreased diversity and to blooms of

opportunistic genera such as *Calpionella* in the late Jurassic and early Cretaceous and *Pithonella* in the Albian-Turonian (18).

The Mesozoic microzooplankton also included diverse species of radiolaria, especially nassellarians, which experienced an evolutionary burst in the Jurassic and Cretaceous periods (2, 115). Tintinnids underwent a similar radiation in the late Jurassic-early Cretaceous period, becoming rare once more in the late Cretaceous (115). The peak of microzooplankton diversity for the Phanerozoic eon seems to have been reached in the Cretaceous period (115).

The Mesozoic record of macrozooplankton is sparse, although chondrophores persist (106). Seven genera of scyphozoans are recorded from the Jurassic Solnhöfen Limestone, including *Rhizostomites* and *Leptobrachites*, and there are also three genera of hydrozoans, at least one of which is preserved in its medusoid stage (*Hydrocraspedota*) (6). Crustaceans were clearly abundant in the Mesozoic plankton although their fossil occurrence is limited to lagerstätten. Enigmatic fossils, found in the stomachs of fish from the Santana formation, have been identified as crab larvae, to which a planktic life habit is attributed (65). Juvenile shrimps, which may also have been planktic, are also preserved in this way, as well as in mass-mortality concretions.

With the exception of radiolarians, all elements of the fossilized calcareous and siliceous zooplankton show high levels of extinction across the Cretaceous-Tertiary boundary. Extinctions were highly selective—more severe in open-water surface dwellers and less severe for inhabitants of deep ocean waters (117). Paul & Mitchell (79) noted that, at both the K-T and Cenomanian-Turonian boundaries, phytoplankton were badly affected. This caused a rapid fall in primary productivity and mass starvation higher up the food chain. Smit & Romein (104) also proposed that the zooplankton were killed by starvation. Survivors among the zooplankton were predominantly small species, and individuals tended to be small even for their species (79).

Cenozoic Era

The enormous wealth of data available for reconstructions of Cenozoic oceanography allows the impact of oceanographic changes on the planktic system to be assessed. It seems likely that the origination of the circum-Antarctic current toward the end of the Miocene set the scene for evolutionary diversification in several microplankton groups through the rest of the Neogene (54). Among microzooplankton, the dominant forms of the Cenozoic era have been foraminifera and radiolaria (115). Tertiary planktic foraminifera are considered to have descended from two small planktic species that survived the Cretaceous-Tertiary decimation (25) and from benthic ancestors (26). Although diversity in Oligocene faunas was limited, the Miocene epoch saw renewed radiation, probably as a consequence of increasing water mass heterogeneity and the development of vertical and lateral gradients (25). Ebridians were common for most of the Cenozoic era (30). Radiolarians show a conspicuous faunal change during the Cenozoic (19).

These changes seem to be linked to radiations in diatoms particularly in the Miocene epoch (112). The two groups compete for silica, and it seems that shallow-, warm-water radiolarians have responded to this competition by becoming lighter (45). The skeletal construction of the deep, cold-water radiolarians has remained unaffected. Tintinnids have a sparse Cenozoic record; examples of well-preserved calcareous forms are known from the Eocene and more rarely the Oligocene epochs, where they occur in association with diverse foraminiferal assemblages (114).

Holoplanktic gastropods are probably Cenozoic in origin. Heteropod and thecosome gastropods became planktic by migration from benthic habits prior to the Eocene. Gymnosomes, ptenoglossans, and nudibranchs are probably Cenozoic in origin as well. All of these groups evolved from benthic ancestors, probably by adult migration (41, 58). Most of the extant groups of planktic crustaceans lack a fossil record but probably migrated into the plankton in the Cenozoic era (88). Salps and thaliaceans are a major soft-bodied component of modern planktic ecosystems, but they have no fossil record and their time of origin is unknown.

During the Cenozoic era, plankton diversity in most groups recovered partially from the end Cretaceous event, but did not return to its former levels (61). Most microplankton seem to have been highly diverse in the Paleocene-Eocene and in the Miocene epochs, with low diversity between. Extinctions were survived preferentially by plankton with simple morphologies, and subsequent radiations produced iterative evolution, with complicated forms arising from these simple stocks (61).

TIMING OF MOVEMENT INTO THE PLANKTON

The previous section demonstrates that migration from the benthos to the plankton has been ongoing for at least the last 650 million years; hence, the planktic realm has never been closed to migration by increased competition for resources or through biotic innovation (Figure 1). Biotic crisis does not precipitate movement from the benthos into the plankton (88), although major oceanographic events may inspire radiations within the planktic cohort (60). For example, diversification in planktic foraminifers in the Mesozoic epoch was coincident with the development of more extensive seas and reduced oceanic circulation (116), but their multiple origins from benthic ancestors appear to have been independent of such a forcing mechanism (26). The zooplankton appear to be unique in the facility with which their composition changes through time. This ability is related to their intense dependence on physical factors for survival, such as water mass stability, temperature, salinity, and upwelling, which have precluded the development of increasingly "better" adaptations [in the sense of Vermeij (121)]. The same phenomenon is reflected today in the paradox of the plankton (43) and identifies the plankton as unique in their macroevolutionary constraints.

BIOGEOCHEMICAL EFFECTS OF THE ZOOPLANKTON THROUGH TIME

The planktic ecosystem contributes major amounts of matter to the seafloor. This matter is derived from the biomass generated in the plankton and from the controls that zooplankton exert on the sinking of small inorganic particles. Of the total flux of particulate matter to the seabed, ≤90% is mediated by zooplankton (76). The main materials derived from the biological activities of the realm are organic carbon compounds and the inorganic skeletal elements of planktic organisms.

Most of the organic matter in the oceans is derived from phytoplankton, and >90% of the plant matter produced is eaten (70), which means that the residue entering various biochemical cycles is the product of metabolism of animals, mainly zooplankton (108). It may now be possible to assess the point in the history of zooplankton when it assumed its modern importance in moving organic material to the seabed and into the sedimentary record. This could represent one of the most important reorganizations of biogeochemical cycles to have occurred in the oceans. It is suggested (63) that the appearance, in the late Precambrian era, of metazoan zooplankton with muscular guts able to produce large fecal pellets radically altered the rate at which organic matter left the water column for the seafloor and, hence, the chemistry of that material when it arrived on the seabed. Late Proterozoic hydrocarbons show isotopic signatures indicative of extensive reworking of organic matter in the water column, whereas later hydrocarbons show signatures indicative of faster rates of migration to the seafloor. This primitive, extensive reworking of material in the water column may have maintained the seafloor in an anoxic condition, promoting the dissolution of carbonate minerals in seawater and raising the carbonate lysocline. Phosphorus at this time would have been recycled in the photic zone and rarely would have reached the seafloor. Faster sinking rates of fecal pellets allowed the seafloor to become oxygenated and facilitated phosphate and carbonate precipitation into increasingly deeper water. Walter (125) proposed that the transition in biogeochemical state occurred in the interval between the deposition of two rock formations, one dated at 590–570 MYA and the other at about 540 MYA, although it is possible that fecal pellets appeared in the rock record much earlier than this (90). It should be noted, however, that Butterfield (16) proposed that elongating food chains within the water column might have increased residence times for organic matter, the opposite effect to that suggested by Logan et al (63).

Many organisms use mineralized hard parts for aggression or defense, and the origin of skeletons precipitated the Cambrian "explosion" of recorded animal diversity. Of 21 types of biologically precipitated inorganic substances, only 4 are commonly found in the holozooplankton: opaline silica, aragonite, calcite, and celestite ($SrSO_4$). Gypsum ($CaSO_4 \cdot H_2O$) may be precipitated by one group of planktic cnidarians (64). Planktotrophic larvae can have phosphatic skeletons, as can pseudoplanktic inarticulate brachiopods (64). Of these six

inorganic compounds, by far the most volumetrically important are carbonates and silica.

Pelagic oozes currently make up 7% of total carbonate mass and 60% of carbonate flux. Since the Mesozoic era, there has been a transfer of mass between shallow and deep marine settings. Southam & Hays proposed (105) that this trend correlates with the rise of planktic calcifers, and modeling suggests that changes in accumulation rate are best explained by a gradual rise in the diversity and abundance of planktic calcifers, including foraminiferids and pteropods in the zooplankton. The model suggests that planktic carbonate was first delivered to the major oceanic basins about 145 MYA and that the total oceanic accumulation rate has been increasing since that time at a rate of ~0.04 × 10^{20} g of calcium per million years (127). It may be that high atmospheric pCO_2 and low $CaCO_3$ saturation in the ocean made surface waters corrosive to potential calcifers during the Paleozoic era (67). However, it is also apparent that deep-water accumulations of carbonate ooze were common in the Paleozoic oceans, based on limestone-dolostone sequence masses (127).

Organisms precipitate calcium carbonate in one of two crystal forms, calcite or aragonite. Aragonite is the less stable of the two in the physical and chemical conditions encountered at the Earth's surface. Heteropod and pteropod molluscs are the only source of aragonite in the open sea, and, in 98% of oceanic regions, this aragonite dissolves before reaching the seabed (32). It is suggested that unexpected alkalinity maxima in midwater may be attributable to this source (32), and these can only have been present since the Cenozoic era.

In modern oceans, most dissolved silica is removed from the water by organisms. It has been carried into the deep sea since the Ordovician radiation of radiolarians, most of which produce an opaline silica skeleton. A major change in distribution pattern is correlated with the radiation of diatoms from the Cretaceous period to the Eocene epoch (66). There is a concomitant change in radiolarian skeletons, which appears to support the suggestion that diatoms are better at removing silica and have reduced its availability to the zooplankton (45). In the modern day, the input of 10^{14} g of dissolved Si per year into the oceans from rivers and mid-ocean ridges is largely balanced by diatom sedimentation (128), and radiolarians contribute only a small amount to silica flux.

DISCUSSION

Members of the zooplankton have migrated into place throughout the late Precambrian era and Phanerozoic eon. The clades of organisms composing the zooplankton have changed significantly over this time, but no major biological innovation appears to have made organisms "better" at being planktic. This facilitates comparison between modern and fossil systems. However, it is important that the chemistry of the oceans has changed significantly with the changing groups of

plankton. Although planktic organisms can be difficult to identify within fossil communities, their study has implications for a wide range of research areas, from macroevolution to biogeochemistry.

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