

Secular Increase in Nutrient Levels Through the Phanerozoic: Implications for Productivity, Biomass, and Diversity of the Marine Biosphere

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Approximately three decades ago, Helen Tappan began a series of classic papers on the interaction of the marine and terrestrial realms, and their influence on nutrient input to the oceans, marine productivity, and plankton evolution and extinction. Unfortunately, many of her assertions conflicted with the fossil record, and her papers have been treated in recent accounts as being largely of historical interest only. Based on recent $\delta^{13}\text{C}$, lithologic, and paleontologic evidence (including a reinterpretation of plankton diversity patterns), I reassess the role of nutrients and productivity in the evolution of the biosphere through the Phanerozoic. Cambrian-to-Devonian seas were characterized by extremely low nutrient ("superoligotrophic") conditions. By the Permo-Carboniferous, nutrient levels and marine productivity had increased toward intermediate ("submesotrophic") concentrations via glaciation, sea level fall, and enhanced deep-ocean overturn and continental weathering. Following end-Permian extinctions, bioturbation rates increased above Paleozoic levels, thereby recycling nutrients back to surface waters (fully "mesotrophic" conditions) and enhancing marine productivity as pelagic habitats expanded (via sea level rise). Increased rates of ocean circulation, continental erosion, and bioturbation further heightened nutrient levels ("eutrophic" conditions) and productivity in the Neogene. Rising nutrient levels and marine productivity may have fueled a secular increase in marine biomass and diversity, and the accompanying decline in background extinction rates, through the Phanerozoic.

INTRODUCTION

In a series of classic papers, Tappan (1968, 1971, 1982, 1986) discussed nutrient input to the marine realm and its role in the evolution and extinction of marine plankton

(see also Bramlette, 1965; Tappan and Loeblich, 1971, 1973; Valentine, 1971; Valentine and Moores, 1970, 1972). She emphasized sequestration of nutrients in terrestrial organic carbon (C_{org}) reservoirs (e.g., coal swamps) and in the deep sea as a result of decreased deep-ocean turnover rates ("nutrient reduction" hypothesis of Erwin, 1993). She concluded that marine primary productivity and atmospheric pO_2 declined, and marine food webs collapsed (e.g., loss of suspension feeders), during the end-Devonian, end-Permian, and end-Cretaceous extinctions as a result; continental rejuvenation and increased ocean circulation were said to reverse these conditions. Unfortunately, many of Tappan's assertions were based on less-detailed stable isotope curves than are now available (cf. Fig. 1) and her interpretations conflicted with the fossil record (Erwin, 1993, p. 228–230; Martin, 1995); consequently, her papers have been treated in recent accounts as being largely of historical interest only or have been ignored altogether.

The record of marine plankton does indeed reflect nutrient levels and productivity in the oceans through time, but not as Tappan (1968, 1971, 1982, 1986) envisioned it. Based on re-interpretation of stable isotope (especially $\delta^{13}\text{C}$), lithologic, and paleontologic evidence, I attempt to reconcile her approach with the geologic record. I speculate that Phanerozoic seas were characterized by a secular trend of increasing nutrient levels, marine productivity (food; cf. Bambach, 1993), biomass, and diversity, and that the rise in marine diversity augmented a decline in background extinction rates through the Phanerozoic.

CAMBRO-DEVONIAN SEAS: PUNCTUATED "SUPEROLIGOTROPHY"

Stable Isotope Evidence

Surface nutrient levels may have been far lower during much of the Cambro-Devonian than those of oligotrophic waters today (e.g., oceanic gyres; Worsley et al., 1986), and

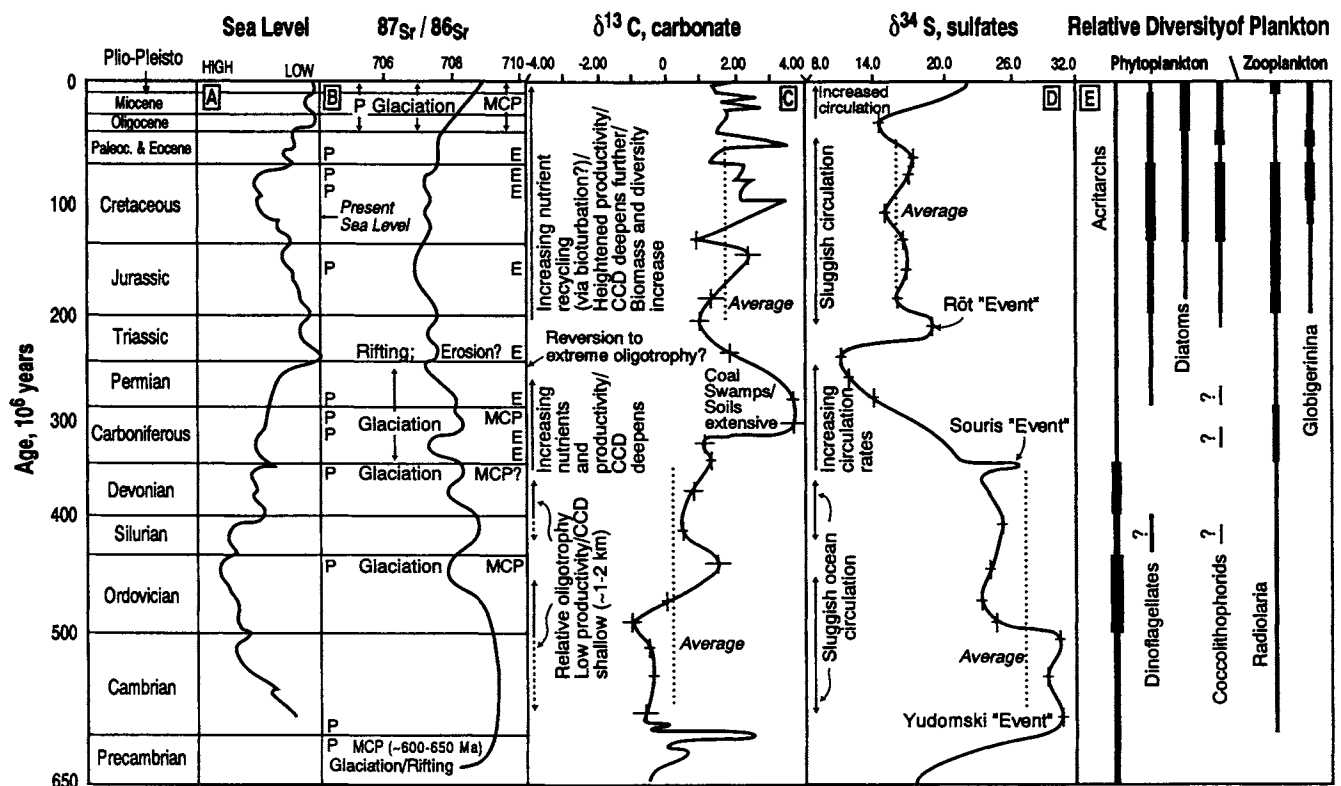


FIGURE 1—Indices of ancient nutrient fluxes and productivity. A) Sea level (Hallam, 1992). B) $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (Hallam, 1992): the greater the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio, the greater the presumed influence of continental weathering (Raymo, 1991) and runoff (Tardy et al., 1989); $^{87}\text{Sr}/^{86}\text{Sr}$ ratios are therefore used herein as indicators of nutrient input to seas from the continents; P=phosphorite peak (Cook and Shergold, 1984); MCP episodes (=eutrophication episodes) after Worsley et al. (1986); E=presumed eutrophication discussed in text (not formally recognized as MCP episodes by Worsley et al., 1986). C) Generalized $\delta^{13}\text{C}$ (primarily from Holser et al., 1988; late Precambrian-Early Cambrian from Magaritz et al., 1986; Cretaceous-Recent after Renard, 1986). Positive values indicate increased marine or terrestrial photosynthesis, whereas negative values indicate decreased productivity or oxidation of marine or terrestrial C_{org} sources (release of ^{12}C -rich CO_2). General shift toward positive values through time suggests heightened photosynthesis that resulted not only from expansion of terrestrial floras (Berner, 1989, 1992), but also increased marine primary productivity as a result of increased C:P burial ratios. See text for discussion of positive $\delta^{13}\text{C}$ spikes in Mesozoic. Averages (dotted lines) fitted visually. D) Generalized $\delta^{34}\text{S}$ (mainly after Holser et al., 1988; "events" after Claypool et al., 1980). High average values in the Cambro-Devonian and Mesozoic suggest extensive SO_4^{2-} -reduction in widespread anoxic basins. Gradual shift toward lower values in late Paleozoic suggests increasing deep-water overturn rates and oxygenation. Pronounced excursions ("events") suggest release into the photic zone of nutrient-rich waters previously stored in anoxic basins (Claypool et al., 1980). See text for discussion of Neogene $\delta^{34}\text{S}$ excursion. Averages fitted visually. E) Relative number of microfossil species (period-averaged data; modified from Martin, 1995).

therefore unable to sustain large phytoplankton populations ("superoligotrophic" conditions; cf. Tappan, 1968, 1971, 1982, 1986). During the Cambro-Devonian, ice caps occurred only in the Late Ordovician and perhaps Early Cambrian and Late Devonian (Frakes et al., 1992); thus, ocean circulation during much of this time was presumably driven by the production of highly saline deep water masses via evaporation in widespread, shallow seaways (Brass et al., 1982). Even in modern oceans, though, in which vigorous oceanic circulation is driven by production of deep-water masses near both poles, dissolved PO_4^{3-} levels in the subphotic zone are several times to an order of magnitude or more higher than in the photic layer (Hallock et al., 1991). Thus, during the Cambro-Devonian, most nutrients may have been sequestered below the photic zone when glaciers were absent (Fischer and Arthur,

1977; Sheldon, 1980; Berner and Raiswell, 1983, p. 860–861; Holser et al., 1988). During much of this interval, too, reduced ocean circulation and widespread anoxia may have resulted in extensive denitrification (reduced NO_3^- concentrations) in the photic zone (Rau et al., 1987) while high sea level trapped nutrients near shore (Holser et al., 1988). Also, continental weathering rates were probably too low during much of the Cambro-Devonian (Knoll and James, 1987) to rejuvenate nutrients in the photic zone (cf. Tappan, 1968, 1971, 1982, 1986; Keller and Wood, 1993).

Low rates of marine photosynthesis and C_{org} burial during much of the Cambro-Devonian are also suggested by relatively light (negative) ratios of ^{13}C to ^{12}C in marine carbonates ($\delta^{13}\text{C}$; Fig. 1). Negative ("light") $\delta^{13}\text{C}$ values indicate decreased productivity or erosion and oxidation of marine or terrestrial C_{org} reservoirs, whereas positive

(“heavy”) $\delta^{13}\text{C}$ values indicate increased marine or terrestrial photosynthesis. Berner and Raiswell (1983) calculated low rates of organic carbon (C_{org}) burial (relative to modern values) for much of the Cambro-Devonian (see also Berner, 1989). As terrestrial floras were not well-established much before the Devonian (e.g., Knoll and James, 1987; Berner 1989, 1992; Horodyski and Knauth, 1994), it is unlikely that erosion of terrestrial C_{org} contributed significantly to the $\delta^{13}\text{C}$ curve much before this time (Raiswell and Berner, 1986; Berner, 1989, 1992).

The hypothesis of low productivity during the Cambro-Devonian is supported by $\delta^{34}\text{S}$ values during this interval (Fig. 1). High $\delta^{34}\text{S}$ values during most of the Cambro-Devonian suggest extensive SO_4^{2-} -reduction, such as in anoxic basins (i.e., decreased deep ocean circulation rates and oxygenation). High $\delta^{34}\text{S}$ values during the Cambro-Devonian presumably resulted from oxidation of available C_{org} by oxyphobic SO_4^{2-} -reducing bacteria (using SO_4^{2-} as electron acceptor). High atmospheric CO_2 levels (Berner, 1993) may have increased C_{org} availability (Garrels et al., 1976) despite low rates of marine photosynthesis. Oxidation of C_{org} by sulfate-reducing bacteria in turn may have contributed to low $\delta^{13}\text{C}$ values (by releasing ^{12}C -rich CO_2) and to extensive anoxia (Berry and Wilde, 1978; Berner and Raiswell, 1983; Raiswell and Berner, 1986; Holser et al., 1988). The overall parallelism between the $\delta^{34}\text{S}$ curve and the cerium curve (which has been suggested as an indicator of paleoredox conditions) for biogenic apatite (conodonts, fish debris, inarticulate brachiopods) corroborates increased anoxia of bottom waters during the early-mid Paleozoic (Wright et al., 1987).

The overall low productivity conditions during the Cambro-Devonian were, however, punctuated by relatively short intervals of heightened nutrient availability. Positive $\delta^{13}\text{C}$ shifts in the Late Precambrian (Vendian) through Early Cambrian (e.g., Magaritz et al., 1986; Kaufman et al., 1993; Brasier et al., 1994), apparently in conjunction with glaciation (Kaufman et al., 1993), suggest increased nutrient availability during this time. A pronounced excursion of $\delta^{34}\text{S}$ to high values (Yudomski “event”; Fig. 1) also suggests mixing into the photic zone of nutrient-rich anoxic waters that may have been stored in isolated basins or deep in the oceans (Claypool et al., 1980; see also Kaufman et al., 1993). Significant biotic turnover also occurred during this interval (see McMenamin and McMenamin, 1990, p. 128–135 and 148–160, for review). The broad Late Cambrian $\delta^{13}\text{C}$ shift (Fig. 1) occurred in conjunction with a major transgression, which may have stimulated marine photosynthesis by releasing nutrients trapped in shelfal sediments (Broecker, 1982; Compton et al., 1993). Positive shifts of the $\delta^{13}\text{C}$ curve in the Late Ordovician and Late Devonian appear to be associated with positive excursions in the $\delta^{18}\text{O}$ curve, glaciation, and sea level fall (Orth et al., 1986; Popp et al., 1986; Stanley, 1988; Brenchley, 1989; Brenchley et al., 1994); another positive $\delta^{34}\text{S}$ shift (Souris “event”) occurred in the Late Devonian (Claypool et al., 1980). The relatively small Late Devonian $\delta^{13}\text{C}$ shift (as opposed to the strong Late Ordovician rise) in the curve of Holser et al. (1988; Fig. 1; cf.

Joachimski and Buggisch, 1993; Algeo and Maynard, 1993) may have resulted from terrestrial C_{org} input during sea level fall (Fig. 1; cf. Raiswell and Berner, 1986; Algeo and Maynard, 1993) or poorly developed glaciers (Frakes et al., 1992) and slowed deep-ocean turnover rates than in the Late Ordovician.

Strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) ratios of marine carbonates suggest that changes in nutrient input from land also contributed to significant changes in $\delta^{13}\text{C}$ through the Cambro-Devonian. Although the initial ratio of ^{87}Sr to ^{86}Sr is the result of radioactive decay of rubidium in igneous rocks, thereafter $^{87}\text{Sr}/^{86}\text{Sr}$ ratios behave like stable isotopes (Holser et al., 1988). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio primarily reflects a balance between weathering of high- $^{87}\text{Sr}/^{86}\text{Sr}$ continental rocks and input of low- $^{87}\text{Sr}/^{86}\text{Sr}$ via hydrothermal exchange between ocean crust and seawater (Raymo, 1991; Jones et al., 1994b). Tardy et al. (1989) used the $^{87}\text{Sr}/^{86}\text{Sr}$ curve as a proxy for continental runoff during the Phanerozoic; they found that the $^{87}\text{Sr}/^{86}\text{Sr}$ curve is in general agreement with calculated runoff rates (a function of latitudinal position of the continents and relative area of continents and oceans; Tardy et al., 1989). Raymo et al. (1988) and Raymo (1994) attributed the overall rise of the $^{87}\text{Sr}/^{86}\text{Sr}$ curve during the late Cenozoic (Fig. 1) to mountain building and dissolved riverine fluxes to the oceans. Similarly, increased $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in the late Precambrian, Late Ordovician, and Late Devonian (Fig. 1), suggest increased runoff (nutrient input) from the continents as a result of orogeny, glaciation, and sea level fall. Soils were also well-developed by the Late Devonian (Knoll and James, 1987), which no doubt increased weathering rates and nutrient flux from the continents by this time (Berner, 1989, 1992; cf. Tappan 1968, 1971, 1982, 1986, and Pitrat, 1970).

Lithologic Evidence: MCP Episodes

Lithologic evidence supports the hypothesis of episodic eutrophication during the Cambro-Devonian. Worsley et al. (1986; see also Sheldon, 1980) recognized a series of step-like increases in Marine Carbon-to-Phosphorus (MCP) burial ratios that presumably reflect increased nutrient availability and permanently enhanced marine productivity (C_{org} burial rates) during the Phanerozoic (Fig. 1). According to this scenario, extensive phosphorite deposition during MCP episodes resulted from intensified recycling of phosphorus (and other nutrients such as nitrogen) back to the photic zone as a result of glaciation, better oxygenation of shallow waters, and enhanced rates of bioturbation (phosphorus “scavenging”; Worsley et al., 1986).

According to these authors, the first MCP episode of the Phanerozoic began in the late Precambrian and extended into the Early Cambrian (~600–650 Ma; Fig. 1; see also Brasier, 1992). This episode is associated with possible glaciation, mixing of nutrient-rich (presumably anoxic) waters into the photic zone (Yudomski $\delta^{34}\text{S}$ Event), and the pronounced positive excursions in $\delta^{13}\text{C}$ described previously (Fig. 1). A second MCP episode (again in associa-

tion with a positive $\delta^{13}\text{C}$ excursion) occurred in the Late Ordovician. Worsley et al. (1986) do not indicate an MCP episode in the Late Devonian, but there is a small rise in the frequency of phosphorites that approximately corresponds to the carbon and sulfur isotope excursions noted previously.

Biotic Evidence

Microfossil and other biotic indices support the above interpretations. Low overall phytoplankton densities during the Cambro-Devonian are suggested (counterintuitively) by the record of acritarch diversity (Martin, 1995). Acritarchs were the dominant phytoplankton of Cambro-Devonian seas (Tappan, 1980), and although of uncertain affinities, are normally considered to be cysts of marine eukaryotic unicellular algae resistant to inimical conditions (Tappan, 1980). Many workers consider high acritarch diversity in ancient rocks to indicate nutrient-rich conditions and high productivity (e.g., Tappan, 1968, 1971, 1980, 1982, 1986; see also Bambach, 1993, p. 390–391), but modern plankton diversity is lowest in nutrient-rich regimes, and, conversely, highest in oligotrophic waters (e.g., Margalef, 1968; McGowan, 1971; Hallock, 1987; Sieser, 1993). Like modern plankton, acritarch assemblages exhibited decreasing diversity in a basin-to-shelf (presumably oligotrophic-to-eutrophic) direction (Tappan, 1980); thus, high cyst diversity prior to the Carboniferous (Fig. 1) may reflect primarily "superoligotrophic" conditions rather than nutrient-rich conditions. These trends are evident in both curves of standing diversity and rates of origination and extinction (Tappan, 1980, fig. 3.24).

Fossil zooplankton also suggest adaptation to overall low phytoplankton densities during much of the Cambro-Devonian. Graptolites appear to have lived in low-oxygen, nutrient-rich waters just below the photic zone, and may have migrated upward to feed on occasional phytoplankton blooms caused by intrusions of deeper nutrient-rich waters into the photic zone (Berry et al., 1987). Conodonts may have lived similarly, as they also exhibited depth-stratification (Clark, 1987). Radiolarians apparently survived by living either in highly productive shallow waters, in oligotrophic oceanic gyres with symbiotic algae, or in deeper subphotic layers of the open ocean as detritivores and bacterivores (Casey, 1993).

Studies of fossil macrobenthos also suggest that food availability was relatively low during much of the Cambro-Devonian. Based on experiments with modern brachiopods, which today characterize oligotrophic habitats, Paleozoic brachiopods had very low food (energy) requirements and were able to survive intervals of starvation of ≥ 2 years (Rhodes and Thayer, 1991). Other relict Paleozoic taxa appear to have low metabolic rates and survive today in oligotrophic refugia (Vermeij, 1987, 1994; Thayer, 1992); food supplies are presumably too low in such refugia to sustain the high metabolic levels of competitors and predators that arose much later (Thayer, 1992; Bambach, 1993; see also VanValen, 1976, p. 206–207).

Intervals of relatively low acritarch diversity during the

Cambrian and Silurian presumably reflect the elevated nutrient levels that followed the late Precambrian-Early Cambrian and Late Ordovician eutrophication episodes, respectively (i.e., abundant nutrients precluded cyst formation; cf. Vidal and Knoll, 1982). Through the Cambrian, following the late Precambrian-Early Cambrian MCP episode, levels of dissolved nutrients presumably declined as they were progressively incorporated into plankton (and other) biomass along food chains. Tiering and diversification of epifaunal suspension-feeders first took place during this time (Bottjer and Ausich, 1986) as plankton presumably became abundant above bottom (Bambach, 1993; Signor and Vermeij, 1994; Martin, 1995). As nutrients were progressively sequestered into biomass, cyst diversity rose to a peak in the Ordovician (i.e., return to low levels of dissolved nutrients; Fig. 1). A similar decrease and increase in acritarch diversity followed the Late Ordovician MCP episode in the Silurian and Devonian, respectively (Fig. 1). Interestingly, the depth and intensity of bioturbation increased during the Early Cambrian, again during the Middle-Late Ordovician (after sea level transgression and presumed nutrient release), and between the Ordovician and Early Devonian (following the Late Ordovician MCP episode; Larson and Rhoads, 1983; Bottjer and Droser, 1994), which suggests greater food (C_{org}) concentrations in sediment in response to elevated surface productivity.

Patterns of acritarch abundance follow those of diversity. Following the late Precambrian-Early Cambrian MCP episode (s), cyst abundance rose to peak levels in the Ordovician ($\sim 100,000$ – $500,000$ cysts/cm³ reported for offshore sediments; Tappan, 1980), but plummeted by the Middle Silurian ($\sim 1,000$ – $10,000$ cysts/cm³ for offshore sediments; Tappan, 1980).

Alternative Interpretations

The interpretation of carbon and sulfur isotope data, especially with regard to the generally low nutrient levels in Cambro-Devonian surface waters, is by no means unequivocal. Low C_{org} burial rates and relatively negative $\delta^{13}\text{C}$ values during much of the Cambro-Devonian could merely reflect the lack of well-developed terrestrial floras prior to the Devonian (Berner and Raiswell, 1983; Raiswell and Berner, 1986; Berner, 1989). Or carbon and sulfur isotope data for the Cambro-Devonian could be interpreted to indicate higher marine productivity (see Brass et al., 1982; van Andel, 1994, p. 207–218). According to the second scenario, warm, saline deep waters would have been unable to hold sufficient oxygen to cause unabated oxidation of C_{org} ; eventually, the oxygen supply in sea water would have had to have run out. When this happened, fewer nutrients would have been released from C_{org} back to the photic zone, and marine productivity and C_{org} formation would have slowed. With less oxygen demand (less C_{org} decay), the oxygen content of deep waters would have increased, and C_{org} decay and nutrient release would have eventually resumed, thereby stimulating productivity. According to this interpretation, C_{org} -rich black shales should

be laminated, with very dark (C_{org} -rich) layers alternating with lighter layers, which is indeed the case for Mesozoic black shales (van Andel, 1994, p. 209).

Early Paleozoic (especially Cambro-Silurian) black shales appear, however, to differ from their Mesozoic counterparts. This is not to deny that heightened productivity may have been important in the generation of some early Paleozoic black shales (e.g., Moore et al., 1993), but these black shales are thicker and were deposited over much larger areas than Mesozoic black shales (Thickpenney and Leggett, 1987). This suggests that anoxia was much better developed during the first half of the Paleozoic than during later times; low oxygen content of ocean waters may have been a relict of low-oxygen conditions left over from the Precambrian (Berry and Wilde, 1978; see also Worsley et al., 1986, p. 258; Worsley et al., 1991, p. 206; cf. Fischer, 1984, p. 143; Des Marais et al., 1992; see also discussion in McMenamin and McMenamin, 1990, p. 161–166) or the result of high CO_2 levels in the atmosphere (Bernier, 1993b). Interestingly, Ingall et al. (1993) and Van Cappellen and Ingall (1994) have suggested that nutrient regeneration is accelerated in *anoxic* waters, but this could have resulted in precipitation of phosphates rather than enhanced recycling of nutrients to the photic zone (cf. Ruttenberg and Bernier, 1993); significant regeneration of nutrients and high productivity during much of the Cambro-Devonian is also not supported by the fossil record (see also Bambach, 1993).

THE PERMO-CARBONIFEROUS

Stable Isotope and MCP Evidence

The trend of increasing marine productivity accelerated in the Permo-Carboniferous with the spread of terrestrial forests, as suggested by the broad rise in $^{87}Sr/^{86}Sr$ ratios; also, Worsley et al. (1986) recognized a fourth MCP episode in the Late Pennsylvanian (Fig. 1; ~300 Ma). Increased rates of terrestrial photosynthesis and continental weathering (cf. Tappan, 1982, 1986, and Erwin, 1993) may have drawn down atmospheric CO_2 , thereby contributing to southern hemisphere glaciation (cf. Raymo, 1991; Kaufman et al., 1993; François et al., 1993), sea level fall, and enhanced ocean turnover rates. Indeed, the gradual shift toward lower $\delta^{34}S$ values during the Permo-Carboniferous (Fig. 1) suggests that extensive southern hemisphere glaciation (Frakes et al., 1992) brought about increased oxygenation as a result of overturn of deep-ocean waters (Berry and Wilde, 1978; Parrish, 1982), which would have coincided with increased nutrient availability in the photic zone. Any positive shift in $\delta^{13}C$ caused by increased *marine* photosynthesis during much of the Permo-Carboniferous was probably swamped, however, by greatly increased rates of terrestrial photosynthesis (Fig. 1; Bernier 1989, 1992, 1993a,b; cf. Małkowski et al., 1989).

Biotic Evidence

The marine fossil record also indicates heightened productivity. After the Devonian, acritarchs are only a rela-

tively minor component of the microfossil record (Fig. 1), which suggests permanently elevated nutrient levels (cf. Tappan, 1968, 1971, 1982, 1986, and Pitrat, 1970). Other biotic evidence suggesting higher nutrient levels and plankton densities after the Devonian includes the decline of the Fusulinacea (benthic Foraminiferida) beginning about the mid-Carboniferous (Tappan and Loeblich, 1988). By analogy to modern larger reef-dwelling foraminifera, the Fusulinacea were adapted to nutrient-poor (oligotrophic) waters (Hallock, 1982; Tappan and Loeblich, 1988). The Fusulinacea were replaced by smaller, rapidly-growing foraminifera during the Middle and Late Permian (Tappan and Loeblich, 1988), and the Fusulinacea themselves tended to *decrease* in size and lose the shell layer known as the keriotheca, which appears to have housed algal symbionts (Ross, 1972), after the Guadalupian (Stanley and Yang, 1994). The prevalence of calcareous algae in Permo-Carboniferous mounds (James, 1983) also suggests elevated nutrient levels (Hallock, 1987) after the Devonian ("sub-mesotrophic" conditions). Increased food supplies beginning in the Carboniferous are suggested by extensive tiering in epifaunal suspension-feeding communities (Bottjer and Ausich, 1986) and increasing depth of bioturbation (Thayer, 1983; Sepkoski et al., 1991), which is energetically costly (Rhodes and Thayer, 1991; Bambach, 1993); i.e., there were relatively reliable food supplies (plankton) high in the water column and deep in sediment (detritus), respectively (Pitrat, 1970; Valentine, 1973, p. 453; Bambach, 1993; Martin, 1995). Moreover, durophagous (shell-crushing) predation increased markedly in the Late Devonian (Signor and Brett, 1984), which hints at lengthening food chains and increasing metabolic rates (Rhodes and Thayer, 1991; Thayer, 1992; Bambach, 1993; Rhodes and Thompson, 1993; see also Vermeij, 1987, 1990).

Permian Reversion Toward Superoligotrophy?

The secular trend of rising nutrient and food availability through the Paleozoic appears to have been ended by a reversion of the oceans toward a superoligotrophic state. The strong negative $\delta^{13}C$ shift in the latest Permian (Fig. 1) was interpreted by Holser et al. (1991) as indicating erosion and oxidation of shelfal C_{org} reservoirs that culminated, at the Permo-Triassic boundary, in well-developed anoxic waters. Anoxia is corroborated by cerium anomalies (Wright et al., 1987; see Erwin, 1993, p. 204–206, for criticisms), but anoxia, by itself, does not appear to have caused the end-Permian extinctions because extinctions occurred before the spread of anoxic waters (cf. Wignall and Hallam, 1992, and Erwin, 1993, p. 242–248). Instead, a lack of ice caps (Frakes et al., 1992), and perhaps also salinity stratification of the oceans (Holser et al., 1991; cf. Erwin, 1993, p. 237–239), may have lowered deep-water overturn rates, so that dissolved nutrients were sequestered below the photic zone as anoxia was developing (cf. Bramlette, 1965; Lipps, 1970, p. 10; Erwin, 1993, p. 156); indeed, only four out of 11 source rocks correspond to upwelling in the Late Permian, whereas three out of four or-

ganic-rich rocks are related to upwelling in the Early Permian (Parrish 1982, 1987).

Like the negative $\delta^{13}\text{C}$ shift during this time, $^{87}\text{Sr}/^{86}\text{Sr}$ ratios also declined. But sea level fall (Fig. 1) and erosion of continents should, seemingly, have *added* nutrients to the oceans, *increased* $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, and *stimulated* marine photosynthesis. There are several possible explanations for this dilemma. First, the Permian was quite arid (Parrish, 1993): based on the low $^{87}\text{Sr}/^{86}\text{Sr}$ ratios for the Permian, Tardy et al. (1989, figures 11–12) concluded that runoff was minimal; moreover, interior drainage may have been extensive (Wyatt, 1984; François and Walter, 1992) because of supercontinent assembly. Second, any strontium delivered to the oceans may have been concentrated in the light isotope because of erosion of extensive basaltic lavas that had been extruded onto the continents (Siberian Traps; Holser and Magaritz, 1987; Holser and Magaritz, 1992, p. 3302). Third, during the Permian, gymnosperm forests were replacing the lycopsids of the Carboniferous. Evergreen leaf litter releases nutrients slowly (Tappan, 1986; Knoll and James, 1987), and may have retarded weathering of continental rocks. Indeed, charophytes, which today live in low-nutrient water (Tappan, 1986), were common in the Permian (Tappan, 1986), and the Fusulinacea re-diversified somewhat after their initial decline (Tappan and Loeblich, 1988).

Other changes in the marine benthos are consistent with lowered productivity. Extinction rates were greater for brachiopods (despite low food requirements) than for bivalves during the end Permian extinctions, apparently because some bivalves also relied upon deposit-feeding (Rhodes and Thayer, 1991). If suspended food supplies decreased during the Permian, deposit-feeding would have become increasingly advantageous (Rhodes and Thayer, 1991; see also Bottjer and Ausich, 1986, and Sheehan and Hansen, 1986). During the Late Permian there may have been a decline in the height of epifaunal suspension-feeding communities (Bottjer and Ausich, 1986), which may have been augmented by biological "bulldozing" of suspension feeders (Thayer, 1983).

THE MESO-CENOZOIC

Stable Isotope Evidence

Carbon isotope values started to rise again in the Triassic, suggesting enhanced marine primary production as a result of the diversification of plankton (Fig. 1). The strontium isotope curve exhibits a sharp rise across the Permo-Triassic boundary and closely approaches the average Phanerozoic value (Fig. 1; Hallam, 1992, p. 171). Despite the overall aridity of the Permo-Triassic, Tardy et al. (1989, fig. 11) indicate a slight rise in continental runoff across the Permo-Triassic boundary, and Holser and Magaritz (1992) suggested increased erosion at this time (see also Kramm and Wedepohl, 1991). Besides erosion, the rise in the strontium curve across the P/Tr boundary is perhaps consistent with upwelling in incipient seaways (associated with rifting of Pangea) or overturn or release

of anoxic marine waters in which terrestrially-derived nutrients may have accumulated (note sharp $\delta^{34}\text{S}$ spike or Röt Event; cf. Yudomski Event; see also Maikowski et al., 1989). Slight rise in the strontium and carbon isotope curves also occurs in the Late Triassic (Fig. 1; Jones et al., 1994a; cf. McRoberts and Newton, 1995).

During the rest of the Mesozoic, the $\delta^{13}\text{C}$ displays a series of sharp positive excursions that correspond to intervals of heightened C_{org} burial (note $\delta^{13}\text{C}$ spikes or Oceanic Anoxic Events = OAEs; Fig. 1). Despite apparently sluggish ocean circulation during the Mesozoic (note $\delta^{34}\text{S}$ average; see also Bralower and Thierstein, 1984; Frakes et al., 1992), enhanced circulation (driven by salinity differences, wind, or submarine volcanism; see Martin, 1995, for references) at times may have stimulated dramatic rises in marine productivity. Indeed, although Worsley et al. (1986) did not recognize any MCP episodes in the Mesozoic (apparently because glaciers were only poorly developed at best; Frakes et al., 1992), extensive phosphorites sometimes occur in the vicinity of OAEs (Fig. 1). Nutrient cycling on shelves may also have accelerated in response to rising bioturbation rates through the Mesozoic (Thayer, 1983; Sepkoski et al., 1991; see also Vermeij, 1987). Expansion of angiosperms in the Cretaceous may have also increased nutrient fluxes to shallow seas, as angiosperm leaf litter decays more rapidly than gymnosperm litter (Knoll and James, 1987; Vermeij, 1987; cf. Tappan, 1982, 1986). Barrera (1994) has suggested increased rates of continental weathering in the Maastrichtian, as well as changes in the $\delta_{13}\text{C}$ curve that may be related to global cooling, sea level fall, and increased marine photosynthesis.

Strong positive excursions in $\delta^{13}\text{C}$ occurred again in the Cenozoic, beginning near the Eo-Oligocene boundary (Shackleton, 1986). These shifts reflect increased marine productivity as a result of formation of polar ice caps, enhanced deep-water overturn, and enhanced continental erosion (through sea level fall) and nutrient input from land (note rise in $^{87}\text{Sr}/^{86}\text{Sr}$ curve; Fig. 1). Also beginning about this time was another series of MCP boosts (Fig. 1). The $\delta^{34}\text{S}$ shift to higher values in the Neogene (Fig. 1), despite *increased* deep-water overturn and presumed oxygenation, suggests that increased C_{org} rain rates combined with falling sea level and sediment influx (rapid burial) to make C_{org} increasingly available for SO_4^{2-} reduction (Canfield, 1991; cf. interpretation of Cambro-Devonian $\delta^{34}\text{S}$ values).

Biotic Evidence

The diversification of marine plankton beginning in the Mesozoic has been attributed to sea level rise and the resultant increase in water column stratification and habitat availability (Lipps, 1970). Among the predominant groups of Mesozoic plankton are the dinoflagellates, which are often preserved as cysts, and the modern representatives of which tend to prefer mesotrophic (intermediate) nutrient levels (Kilham and Kilham, 1980). Unlike acritarchs, then, diversification of dinoflagellate cysts during the Mesozoic may signal *heightened* nutrient levels (although not as high as today's; Bralower and Thierstein,

1984) that may have fueled the rise in plankton diversity as pelagic habitats reappeared. Diatoms, which today prefer nutrient-rich ("eutrophic") conditions (Kilham and Kilham, 1980), diversified explosively in the Miocene (Tappan, 1980) in response to further eutrophication. Bioturbation rates continued to rise through the Cenozoic (Thayer, 1983; Sepkoski et al., 1991), presumably in response to increasing surface productivity.

One reviewer suggested that intensive bioturbation in modern reef (oligotrophic) environments (e.g., Walter and Burton, 1990) is inconsistent with the scenario of a coupled rise in surface photosynthetic (C_{org} rain) rates and bioturbation rates through the Phanerozoic. This simply reflects the insidious bias of uniformitarianism (an *investigator* bias that might be called the "pull of the Recent" if the phrase had not been pre-empted for other biases; e.g., Raup, 1976). Modern environments differ from ancient ones in both obvious and *subtle* ways. In the case of modern reefs, bioturbation rates are relatively high in what we view as nutrient-poor environments *today* because these rates have increased through the Phanerozoic as overall surface productivity in the oceans (and C_{org} rain rates to the bottom) have increased. Ancient reef settings were presumably even more nutrient-poor ("superoligotrophic") earlier in the Phanerozoic, and bioturbation rates were correspondingly lower (Thayer, 1983; Sepkoski et al., 1991).

The rise in productivity in the Meso-Cenozoic was accompanied by a dramatic rise in abundance and diversity of the bivalve-rich Modern Fauna (Kidwell, 1990; Bambach, 1993; another kind of "pull of the Recent"). Dominance of the Modern Fauna in the Meso-Cenozoic is not entirely the result of taphonomic bias or increased provinciality (Signor, 1985). Modern bivalves require much higher food levels than do modern brachiopods (Rhodes and Thayer, 1991). The diversification of the Modern Fauna began in Cambro-Ordovician nearshore environments, where nutrients were presumably concentrated, after which it radiated into progressively deeper habitats, presumably in response to increasing nutrient (food) availability away from shore (Bambach, 1993). Interestingly, the locus of siliceous ooze deposition also shifted across the shelf during the Phanerozoic, with radiolarians eventually giving way to diatoms (Maliva et al., 1989; see Martin, 1995, for further discussion); calcareous plankton appear to have followed a similar path, which may account for enigmatic occurrences of calcareous nannofossil-like objects from the Paleozoic (Fig. 1; Martin, 1995; see also Boss and Wilkinson, 1991). Rising food levels in the Mesozoic may have also permitted reefbuilding taxa to sustain growth rates sufficient to build multiserial skeletons necessary for extensive photosymbiosis (Wood, 1993), and the diversification of anti-fouling predators and grazers that may have contributed to the success of reef ecosystems (Vermeij, 1987, 1994; Wood, 1993; Martin, 1995).

UPWARD SCALING OF ECOLOGICAL PROCESSES AND RECONCILIATION OF TAPPAN'S SCENARIO WITH THE GEOLOGIC RECORD

Upward scaling of ecological processes to geological (evolutionary) time scales is one of the principle limita-

tions to interpreting ancient fossil assemblages (cf. Aronson, 1994). Processes of ecologic succession, for example, are not necessarily equivalent to those of community evolution (e.g., Miller, 1986), and such an approach must be used with caution, as it is potentially misleading. Indeed, based on a strict analogy of ecologic succession proposed by some workers (e.g., Odum, 1969), Tappan (1971) described a sequence of Phanerozoic communities that was at odds with the fossil record. According to her (1971), "youthful" marine ecosystems are characterized by high primary productivity, low "nutrient conservation" (low rates of nutrient recycling), low diversity, an emphasis on "r-strategies" (opportunism), and relatively short food chains. "Mature" ecosystems, on the other hand, are characterized by low primary productivity and high "nutrient conservation", high species diversity, an emphasis on "k-strategies" (slow growth, delayed reproduction), and relatively long food chains. According to Tappan (1971), ecosystems matured during the Paleozoic: food chains became more weblike and the biomass (carrying capacity) of the global marine ecosystem increased (productivity/biomass ratio decreased). As argued herein, however, in the post-Devonian Paleozoic, relatively long food chains with well-developed predators (characteristic of "mature" ecosystems) were sustained by elevated nutrient recycling (characteristic of "mature" ecosystems) and relatively *high* marine productivity (characteristic of "youthful" ecosystems). The Permo-Carboniferous was characterized by glaciation, enhanced ocean overturn, sea level fall, and extensive soil formation (Fig. 1), all of which would have heightened nutrient input, primary productivity, and biomass in the photic zone (c.f. Tappan, 1970; and Pitrat, 1970). By contrast, Cambro-Devonian seas were largely characterized by relatively low nutrient recycling ("youthful" ecosystems) and *low* productivity ("mature" ecosystems), which were able to sustain only relatively short food chains ("youthful" ecosystems).

BIOMASS, DIVERSITY, AND EXTINCTION THROUGH THE PHANEROZOIC

The rising diversity of the Modern Fauna through the Phanerozoic was accompanied by a decline in background extinction rates (Raup and Sepkoski, 1982). This decline has been attributed to the accumulation of geographically widespread (environmentally tolerant), species-rich clades through time (e.g., Flessa and Jablonski, 1985; see also Vermeij, 1987, p. 400-401). The record of marine plankton suggests that marine biomass and diversity were also being ratcheted upward through the Phanerozoic by a steplike rise in nutrient (food) availability (Benton, 1979; Ulanowicz, 1980; Bambach, 1993; cf. Van Valen, 1976; Schidavski, 1991). McMenamin and McMenamin (1994, p. 225-226) proposed a similar mechanism to account, in part, for increasing terrestrial plant biomass and diversity through the Phanerozoic.

Catastrophic fluctuations in nutrient levels described herein appear to coincide with a number of mass (and minor) extinctions described by Sepkoski (1986, 1992), and

may have exacerbated extinctions via shortening of pelagic food chains (Martin, 1995; Martin, in press). Nevertheless, re-expansion of the marine biosphere after each extinction resulted in a secular trend of rising marine diversity that may have augmented the decline in background extinction rates through the Phanerozoic. Survivors ("opportunists") of extinction would have been prone to higher reproductive rates. Thus, following each extinction, nutrients recycled to the photic zone were incorporated into larger amounts of biomass (permanently increased C:P ratios), and larger populations of organisms (Bambach, 1993); because of their larger populations, species were better able to exploit available niches (including marginal marine environments; cf. Vermeij, 1987, p. 400–401), and diversify into new taxa. Metabolic rates of taxa also appear to have increased through time (Vermeij 1987, 1994; Thayer, 1992) in response to enhanced food availability (Bambach, 1993; Martin, 1995).

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