15

Does Phytoplankton Cell Size Matter? The Evolution of Modern Marine Food Webs

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Many physiological rates and ecological and evolutionary patterns are affected by the size of organisms involved; for example, metabolic rate, elemental requirements, sinking rates, abundance, biomass, diversity, home range, and longevity (Smayda 1970; Shuter 1978; Peters 1983a; Agusti *et al.* 1987; Bonner 1988; Kiorboe 1993; Brown 1995; Stemmann *et al* 2004) As the foundation of aquatic food webs, the size of the cells that compose the phytoplankton community has a fundamental influence on the structure and function of aquatic ecosys-tem (Figure 1). In this chapter, I review the relationship between organism size and met-abolic rate and the resulting consequences for ecological patterns of abundance, diver-sity, and food web structure and function; summarize the current state of knowledge of how phytoplankton community size structure has changed over geological time; and explore the potential consequences of macroevolutionary shifts in phytoplankton community size structure to the evolution of food web assembly, structure, and func-tion over geological time.

I. SIZE MATTERS: FROM PHYSIOLOGICAL RATES TO ECOLOGICAL AND EVOLUTIONARY PATTERNS

A. Size Scaling of Physiological Rates

"Almost all aspects of the life of a phytoplankton cell are influenced. more or less. by its size . The mechanisms underlying the size-dependent patterns have undoubtedly steered the general course of phytoplankton evolution, but the organisms that do not abide by the rules reveal the wonder ful diversity of ways in which cells have managed to disobey the 'laws' scripted for them' —Chisholm 1992

Size scaling laws are a remarkably general and widely observed phenomenon in biology (Kleiber 1947; Peters 1983a; Bonner 1988; Brown 1995; Kerr and Dickie 2001) The most fundamental is the relationship between an organism's size and its metabolic rate because this governs the rate of the individual's interaction with the environment (Peters 1983a; Brown 1995). From bacteria to large mammals, body size can be used to predict metabolic rate:

$$B = B_0 M^b \tag{1}$$

where b is the size scaling exponent of the relationship between the metabolic rate (B) and the organism's size (M) (see Figure 1). The size scaling exponent tends to be ¾ under standard temperature and optimal growth conditions due to the geometric constraints of transportation networks within organisms (Banavar *et al.* 2002). Phytoplankton cell volumes span 10 orders of magnitude; assuming $b = ¾$, then, phytoplankton size can account for ~6 orders of magnitude in metabolic rate A large variety of size scaling exponents have been reported from field and experimental observations of the metabolic rates of phytoplankton (Banse 1976; Taguchi 1976; Schlesinger *et al* 1981; Sommer 1989; Finkel 2001) When resource or energy supply does not match the demands of growth, and the acquisition of resources is size dependent (such as light-harvesting and nutrient diffusion in phytoplankton), then the size scaling exponent b changes with resource availability (Finkel and Irwin 2000; Finkel 2001; Finkel *et al* 2004). Regardless of the explanation, or the exact exponent, the size dependence of metabolic rates appears to influence many fundamental macroecological and
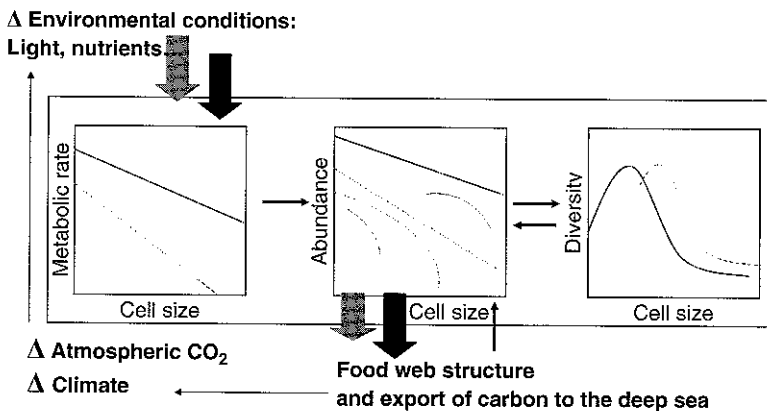

FIGURE 1   The interrelationships between climate, the size scaling of metabolic rate, abundance, and diversity of phytoplankton The dark lines represent before a change in climate and the lighter grey arrows and dashed lines represent after a change in climate

evolutionary patterns (Gould 1966; Peters 1983a; Bonner 1988; Brown 1995; Kerr and Dickie 2001; Niklas and Enquist 2001; Trammer 2002; Irwin *et al* 2006)

B. Size–Abundance Relationship

Classic studies on marine plankton indicated that the abundance (A) of organisms per unit volume or area is often inversely related to organism mass:

$$A = cM \qquad (2)$$

where the size scaling exponent (ξ) is often approximately −1 (see Figure 1) (Sheldon and Parsons 1967; Sheldon *et al* 1972), such that biomass per unit volume or area is the same for all logarithmically separated size classes. Subsequent field and lab studies have documented considerable variability in the size scaling exponent associated with marine phytoplankton communities, ξ, often ranging from − 2/3 to − 5/3 (Agusti 1987; Agusti and Kalff 1989; Boss *et al* 2001) Small phytoplankton cells often dominate in stable, oligotrophic environments such as the open ocean, whereas larger cells increasingly dominate in eutrophic environments that are characterized by environmental variability, such as coastal areas (Malone 1971; Peters 1983b; Sprules and Munawar 1986; Chisholm 1992; Li 2002). This suggests that both ξ and the intercept *c* increase with limiting resource availability (or chlorophyll concentration) (Peters 1983b; Sprules and Munawar 1986; Chisholm 1992; Duarte *et al* 2000; Li 2002). The changes in size structure with resource availability and total biomass have often been interpreted as a release from grazer control (Malone 1971; Armstrong 2003; Irigoien *et al* 2004; Morin and Fox 2004) Competition (Grover 1989, 1991), deviations from steady-state (Sprules and Munawar 1986), and the scale-free self-organization of complex adaptive systems (Rinaldo *et al* 2002) have also been proposed as mechanisms to explain the size scaling of

abundance, but none of these hypotheses explains the increasing dominance of large cells under high nutrient conditions. Alternatively, it has been demonstrated that the size scaling of cellular nutrient requirements and growth can explain the power-law relationship between cell size and abundance, the dominance of small phytoplankton cells under oligotrophic conditions, and the relative increase in abundance of larger phytoplankton cells under eutrophic conditions (Irwin *et al* 2006)

C. Size–Diversity Relationship

Species diversity (S, number of species) is often a skewed log-normal function of organism size, where maximum species diversity for the log-normal distribution occurs at an intermediate organism size (see Figures 1 and 2) (Van Valen 1973; May 1978; Fenchel 1993; Brown 1995; Gaston and Blackburn 2000). There are known deviations from this relationship; some taxonomic groups have several peaks in diversity at different sizes, or diversity can be independent of organism size (Gaston and Blackburn 2000). Although the majority of the pioneering work on the size–diversity relationship has focused on mammals and birds, Fenchel's compilation of 18,500 aquatic free-living species, including bacteria and protozoa, indicates intermediate-sized species are most diverse in marine and freshwater habitats (Fenchel 1993) An analysis of the size distribution of phytoplankton species from the Provosili-Guillard national culture collection indicates that phytoplankton species diversity may also be a skewed log-normal function of cell size (Figure 2). The data available may be biased due to sampling techniques and sampling effort; for example, documentation of the diversity of picoeukaryotes has increased dramatically with the recent application of molecular techniques to identify species from field assemblages (Moon-Van Der Staay *et al* 2001; Not *et al*

FIGURE 2. An analysis of the size distribution of all phytoplankton species with size information from the Provasoli-Guillard national culture collection of marine phytoplankton indicating phytoplankton species diversity may be a skewed log-normal function of cell size (see Figure 1).
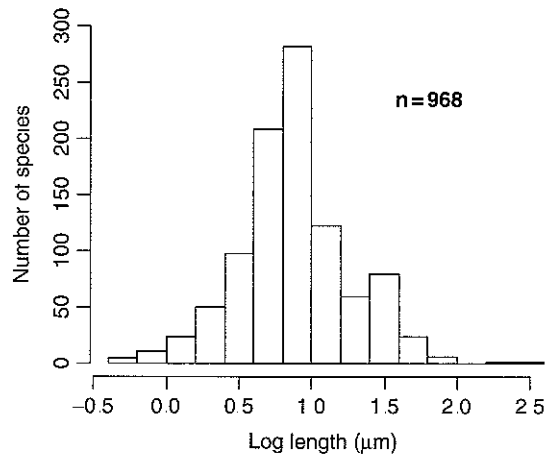
2002; Vaulot et al. 2002). Similar discoveries of cryptic diversity across all size classes of phytoplankton may follow as these techniques are applied equally to the whole phytoplankton community. The recent demonstration that phytoplankton species richness scales with habitat area (Smith et al. 2005) suggests there may also be a relationship between habitat size and size structure of phytoplankton communities Ideally, a global database of current phytoplankton diversity and associated cell size should be compiled. Many hypotheses have been proposed to explain the pattern in the size scaling of diversity; the most likely factors include the size scaling of origination (Gillooly et al. 2005) and extinction rates (Norris 1991) as a function of different environmental and ecological conditions over the history of the taxonomic group (Stanley 1973b; Dial and Marzluff 1988; McShea 1994).

D. Size Matters: Food Web Structure and Function

1. Functional Composition of the Marine Food Web

Early descriptions of marine feeding relationships focused on the relationship among nutrient concentrations, phytoplankton and zooplankton, and the transfer of primary production to organisms of human interest such as fish (Ryther 1969)

Improvements in the measurement of bacterial abundance have led to the increasing recognition of the importance of bacteria in the marine food web. Bacteria consume dissolved organic matter, stimulate recycling of organic matter, and provide fuel for a variety of small heterotrophs (protozoan ciliates and flagellates) that can be consumed by larger zooplankton and transferred to higher trophic levels (Pomeroy 1974; Azam et al 1983). The grazer food chain (phytoplankton, zooplankton, fish) and the microbial food web have often been studied independently, but their integral coupling and resulting influence on the partitioning of matter and energy is widely recognized (Azam et al. 1983, 1993; Sherr and Sherr 1994; Thingstad and Hagström, 1997). Accumulating evidence indicates that marine viruses (and perhaps archaea and pathogenic bacteria) also appear to play an important role in the planktonic food web, altering the turnover time of different organisms and affecting the supply of dissolved organic material to bacteria (DeLong and Karl 2005; Suttle 2005).

2. Big Things (Often) Eat Smaller Things

Although there are many individual exceptions, the hierarchical size differences

between consumers and their prey is the basis of the strong relationship between organism size and trophic level within the food web (Dussart 1965; Parsons and Takahashi 1973; Sieburth et al 1978; Cohen et al. 2003; Jennings and Mackinson 2003) (Figure 3). Meta-analyses of aquatic and terrestrial systems suggest that for a majority of animal species in natural food webs, a larger predator consumes a smaller prey (Cohen et al. 1993). The size difference between predator and prey may be smallest in the microbial web where bacteria (~1 μm) are consumed by ciliates and flagellates (many of which are between 5 and 20 μm) (Sherr and Sherr 1994). Small heterotroph grazers can be consumed by larger zooplankton and can contribute to food webs with 5 or more trophic levels (Sherr and Sherr 1994; Link 2002). In comparison, a grazing food web dominated by phytoplankton (10–100 μm) should result in food webs with relatively few trophic levels because the phytoplankton are too big for most flagellate and ciliate grazers and instead are prey for larger zooplankton such as copepods (0.2–28 mm) (Huys and Boxshall 1991), which are often a direct food source for fish (Ryther 1969). Each trophic transfer is associated with

large losses (> 80%) of matter and energy (Parsons and deLange Bloom 1974; Cohen et al. 1993, 2003; Jennings and Mackinson 2003), so food webs dominated by the microbial food web will theoretically result in a decrease in matter and energy transfer to higher trophic levels

Larger individuals often consume prey with a larger range of masses than smaller predators (increased diet breadth) (Cohen et al. 1993, 2003; Hansen et al. 1994) and as a result the predator to prey mass ratio tends to change with increasing body mass of the predator (Cohen et al. 1993; Jonnson and Ebenman 1998). This increase in the breadth of available prey with increasing size of the consumer has profound consequences for food web structure. Models indicate that changes in the predator–prey body size ratio with predator size can affect the resilience and probability of stability of Lotka–Volterra food chains of more than three trophic levels (Jonnson and Ebenman 1998). An increase in the breadth of prey masses consumed by larger predators will tend to increase the connectance (proportion of total possible binary trophic links) in the food web. Increases in connectance and species diversity will tend to decrease
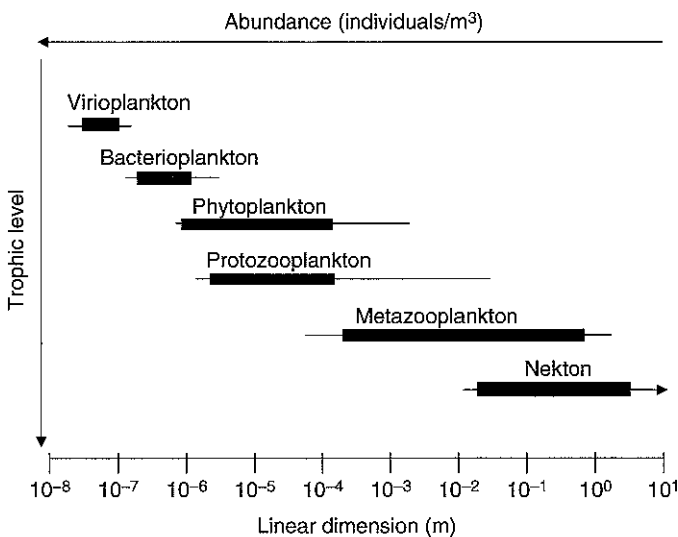

FIGURE 3 Size, abundance, and trophic structure of the planktonic marine food web. Adapted from Sieburth et al 1978

the strength of interaction between predator–prey pairs and generally increase the complexity of the food web (Cohen *et al* 2003; Woodward *et al* 2005).

There is considerable evidence that many phytoplankton grazers discriminate between prey based on differences in size as well as nutritional quality or toxicity (Mullin 1963; Parsons *et al* 1967; Irigoien *et al* 2000, 2003; Teegarden *et al* 2001). For example, *Calanus finmarchicus*, a main food source for many commercially important fish, has a general preference for diatoms relative to ciliates and smaller phytoplankton species (Irigoien *et al*, 2003). In general, it is assumed that a predator has a Gaussian-type preference for prey of a certain size (Hansen *et al* 1994; Loeuille and Loreau 2005). Experimental measurements of the size selectivity of protozoan predators on bacterial prey do appear to be unimodal, but the acceptable prey size range varies considerably among predators (Chrzanowski and Simek 1990; Hansen *et al* 1994). It seems credible that most predators will have sharp upper and lower size boundaries beyond which they cannot physically consume prey, depending on the feeding apparatus, creating size refugia that can cause complex patterns in food web structure (Chase 1999). For example, the adult females of the marine copepod *Calanus pacificus* cannot effectively consume diatoms with diameters less than 3.8 μm, and below a certain biomass concentration of prey, ingestion rate (mg C/copepod/time) is greatest for larger diatoms (Frost 1972)

3. Organism Size and Trophic Cascades

Field observations and theoretical approaches suggest that it is possible that the size selectivity of predators for prey can cause a coincident cascading change in the size distribution of all organisms in the food web Brooks and Dodson (1965) discovered that small- to medium-sized lakes with populations of the zooplankton predator *Alosa* (commonly known as the alewife) were characterized by much smaller-bodied zooplankton populations than lakes that lacked functionally similar fish populations. They hypothesized that predators prefer the largest possible prey that can be consumed and that larger zooplankton species are more metabolically efficient than smaller zooplankton. There is some evidence that marine bacteriovores selectively feed on larger, faster growing bacteria, altering the size structure of the standing stock bacteria (Gonzalez *et al* 1990) Although this size efficiency hypothesis provides a consistent explanation for the patterns in zooplankton populations in the lakes of southern New England, the proposal that larger zooplankton are metabolically more efficient has been questioned (Peters 1991, 1992; Hopcroft *et al* 2001), and the theory has generally failed to predict the abundance and size structure of phytoplankton and zooplankton in larger lakes and the ocean (Brooks and Dodson 1965; Frank *et al* 2005; Scheffer *et al* 2005) The increase in the diet breadth of larger zooplankton provides a potentially simpler alternative explanation for the relatively high abundance of larger versus smaller zooplankton under low predation pressure (Brooks and Dodson 1965; Cohen *et al* 2003) The prevalence of omnivory and high connectance (Link 2002) and low interaction strength between individual predator–prey pairs may contribute to the relative rarity of trophic cascades in marine food webs (Scheffer *et al* 2005) These differences may lessen as we continue to "fish down the food web" (Pauly *et al* 1998)

The once cod-dominated northwest Atlantic food web now shows evidence of a trophic and size cascade where the removal and subsequent lack of recovery of the cod, *Gadus morhua*, as well as a large number of other predatory fish, is associated with an increase in the abundance of smaller pelagic fish and benthic macroinvertebrates, most

notably the northern snow crab and shrimp (Worm and Myers 2003), a decrease in abundance of small-bodied invertebrates, a slight increase in the abundance of phytoplankton, and a corresponding decrease in surface nitrate concentrations (Frank *et al.* 2005) This is in contrast with the majority of observations in the surface ocean that show a strong correlation between low nitrate (or light, phosphate or iron) concentrations and low chlorophyll concentrations It seems probable that there is similar potential for a dynamic change in the standing stock and size of phytoplankton in response to the change in limiting nutrient concentration that could then transfer up the food web where the size of the organisms within each trophic level is the outcome of the dynamic interaction of environmental conditions that affect net photosynthetic production, the size structure of the phytoplankton community, and size-selective predation of organisms in the upper trophic levels Mesocosm enrichment experiments in the oligotrophic coastal Mediterranean support this hypothesis: increasing nutrient inputs resulted in an increase in the relative abundance of large phytoplankton and the ratio of phytoplankton to heterotrophic biomass (Duarte *et al* 2000) Meta-analyses of food webs strongly support the assertion that both bottom-up and top-down processes control real food webs Primary production determines the biomass in all trophic levels and top-down processes generally weaken with each trophic level and are often not observable at the base of the food web (Brett and Goldman 1996) The generally weak effect of trophic cascades at the base of the food web may be due to nutrient contributions from consumers (excretion, sloppy feeding, etc) from all trophic levels (Attayde and Hannsson 2001) Much more work is required to determine the size selectivity of predators for their prey, especially with and without the presence of multiple prey, predators and their higher-level consumers

II. RESOURCE AVAILABILITY, PRIMARY PRODUCTION, AND SIZE STRUCTURE OF PLANKTONIC AND BENTHIC FOOD WEBS

In modern marine food webs, there is often a strong coincident association among resource availability, primary productivity, total chlorophyll, export production, and the size structure of the phytoplankton community When light and inorganic nutrients are abundant, as in coastal and upwelling zones and eddies, total chlorophyll tends to be high and large phytoplankton cells are abundant In contrast, when light and nutrient availability are low, such as in the oceanic gyres or the iron-limited high-nutrient low-chlorophyll regions, phytoplankton communities are dominated by extremely small picoplankton (Malone 1971; Falkowski *et al* 1991; Chisholm 1992; Le Bouteiller *et al* 1992; McGillicuddy and Robinson 1997; Le Borgne *et al* 2002; Li 2002; Sweeney *et al* 2003) This general trend is supported by vast amounts of field data; for example, more than a decade of data collected predominantly from the North Atlantic documents clear increases in the abundance of large phytoplankton and decreases in the abundance of small picoplankton with increasing bulk chlorophyll concentration in the surface ocean (Li 2002) Environmental conditions such as temperature can have different effects on the grazing versus the microbial food web and the transfer of carbon through the food web and export of particles to the deep sea (Pomeroy and Deibel 1986; Pomeroy *et al* 1991)

Field evidence strongly supports a strong correlation between the increase in primary production and chlorophyll standing stock with corresponding changes in planktonic and benthic primary and secondary consumers Large phytoplankton cells tend to be grazed by large zooplankton (Steele and Baird 1961; Mullin 1963; Sherr and Sherr 1994; Savenkoff *et al* 2000) In contrast,

when smaller phytoplankton species dominate the autotroph community, heterotrophic dinoflagellates, ciliates, and smaller zooplankton can come to dominate the zooplankton community (Sherr and Sherr 1994; Savenkoff et al. 2000). In the equatorial Pacific, the long-term monitoring at the Hawaiian Ocean Time Series documents long-term oscillations in the taxonomic structure of the phytoplankton community from small cyanobacteria to larger eukaryotes (Karl 1999). Cyanobacterial dominance of the phytoplankton community is associated with the low availability of fixed nitrogen, low export flux, and famine in the benthic community on the underlying abyssal plane. In contrast, the dominance of the phytoplankton community by larger eukaryotic phytoplankton species is associated with higher population abundance and increases in the size of the organisms in the benthos (Smith et al. 1997; Karl 1999; Smith et al. 2002).

There is a well-established global association between increases in resource supply (water-column depth, distance from coast) and the size of benthic communities (Thiel 1975; Brown et al. 2001). Specific positive associations have been established between the magnitude of phytoplankton export and the abundance and size of benthic organisms such as nematodes in the central equatorial Pacific (Brown et al. 2001). The extremely tight correlation between equatorial upwelling, primary productivity, export production, and macrofaunal abundance led to the hypothesis that changes in primary productivity on decadal or greater time scales could yield profound changes in deep-sea benthic communities that may be evident in the fossil record (Smith et al. 1997).

The interaction between organisms and their environment have resulted in large-scale changes in the size of phytoplankton and marine invertebrates over time (Hallam 1975; Bambach 1993; Schmidt et al. 2004; Finkel et al. 2005; Huntley et al. 2006). The size of organisms in the food web affects a number of the primary descriptors of food web structure and function, including species abundance and diversity (S), the number of trophic links, the minimum and maximum number of trophic levels or trophic height, connectance (C, proportion of total possible binary trophic links present in the food web), and complexity (S*C) (Brown and Gillooly 2003; Cohen et al. 2003; Woodward et al. 2005). Limited paleodata do not permit detailed or complete analyses on all these descriptors; nonetheless, application of the main physiological and ecological principles of the effects of organism size on food web structure and function may provide additional insight into the evolutionary history of marine food webs from observations of changes in the size structure of fossil phytoplankton and zooplankton assemblages.

III. SIZE AND THE EVOLUTION OF MARINE FOOD WEBS

A. Increase in the Maximum Size of Living Organisms Through Time

The maximum size of living organisms has increased over geological time (Bonner 1988). Life began as prokaryotic microbes. Eukaryotic phytoplankton, which become increasingly dominant in the deep Proterozoic, are often larger and morphologically more complex than the fossils of cyanobacteria, which dominated the phytoplankton in the Paleoproterozoic and Mesoproterozoic (Knoll et al. 2006; Knoll et al., Chapter 8, this volume). The origination of new faunal groups is frequently associated with an increase in the maximal body size (Gould 1966). For example, the transition to the Ediacaran fauna (575–543 million years ago [Ma]) introduced a number of organisms that ranged from centimeters to ~1m in the case of Dickinsonia (Carroll 2001). The largest organisms to date are the flowering plants, with their origins in the Cretaceous. There is some suggestion that this trend does not

extend indefinitely but saturates once the disadvantages of getting larger can no longer be overcome by the advantages of an increase in complexity (Bonner 1988).

## B. Organism Size Within Lineages Through Time (Cope's Rule)

It has been suggested that the fossil record documents an evolutionary tendency for taxonomic groups to evolve toward larger physical size, commonly termed Cope's rule (Newell 1949; Nicol 1964; Stanley 1973b; Pearson 1998). Although there are numerous counter-examples (Stanley 1973b), secular increase in organism size has been documented in a wide variety of organisms including foraminifera (Norris 1991; Kaiho 1999), ammonites and bivalves (Hallam 1975), and many vertebrate groups (Cope 1885; Nicol 1964; Alroy 1998). Several different hypotheses have been postulated to explain the evolutionary tendency toward larger organism size within lineages, including: competitive advantage over siblings (Castle 1932), improved ability to capture food or avoid predation, increased intelligence, greater reproductive success, extended individual longevity (Stanley 1973b), and increased complexity (Bonner 1988). The most parsimonious explanation for Cope's rule is the tendency for higher extinction rates for larger versus smaller species after a perturbation, such as a mass extinction, followed by speciation. Species radiation in conjunction with passive evolutionary mechanisms will tend to result in increases in both the maximum and minimum size, with no change in the mean body size of the group (Stanley 1973b; McShea 1994; Gould 1997; Pearson 1998). In other words, species radiation within a group will often result in an increase in the diversity and size range within a lineage, with or without specific size-dependent selection pressures (Stanley 1973b; McShea 1994; Gould 1997). If external environmental or biological factors select for species of a specific size, there will be a corresponding change in the average

size of the species within the lineage through time. A combination of size bias in origination or extinction, physiologically imposed boundaries on minimum and maximum size, and active selection pressures can result in complex temporal patterns in the evolution of body size (McShea 1994). Furthermore, different selection pressures may act on individuals of different size, resulting in a large variety of size distributions within a lineage (Carroll 2001).

C. Climatically Driven Macro-evolutionary Change in Organism Size

Macroevolutionary change in organism size can be a dynamic response of size-dependent selection in response to temporal changes in environmental forcing (Stanley 1973b; McShea 1994; Finkel et al 2005). For example, a recent examination of marine planktonic diatoms found that the extreme minimum and maximum size of the diatom frustule has expanded in concert with species diversity through the Cenozoic, but the average size of the diatom frustules within the communities is highly correlated with climate change (Figure 4) (Finkel et al 2005). The average size of the diatoms has followed changes in the vertical temperature gradient in the tropical ocean; an indicator of both the stability of the water column and the average temperature gradient between the equator and poles (Wright 2001; Zachos et al 2001). The thermal gradient affects the availability of light and nutrients in the surface ocean, altering the types of niches available to plankton and other marine organisms (Rea 1994; Rutherford et al 1999; Zachos et al 2001; Schmidt et al 2004; Finkel et al 2005). The macroevolutionary changes in the size of diatom frustule over the Cenozoic are consistent with size changes observed for single species of marine diatoms in response to temperature and upwelling zones over hundreds of thousands to several millions of years (Wimpenny 1936; Burckle and McLaughlin 1977; Burckle et al 1981; Sorhannus et al 1988)

FIGURE 4. The average size of the frustule of the dominant marine diatom species (± 1 standard error, dotted line) through the Cenozoic. Modified from Finkel et al. 2005
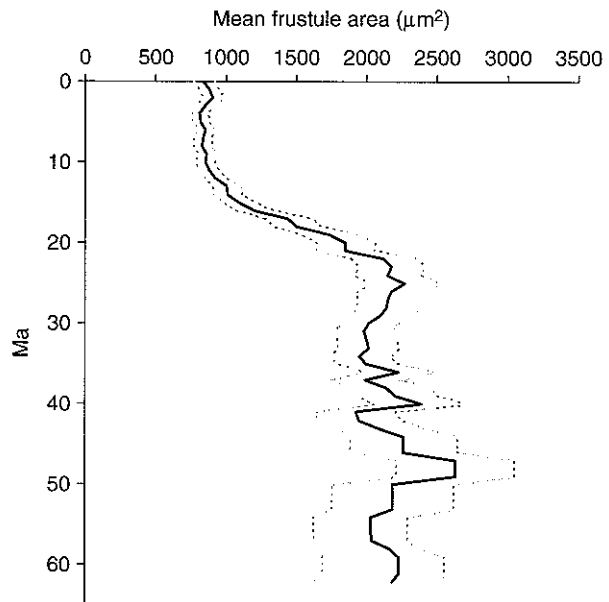
Zooplankton groups also exhibit size changes that correspond to changes in water-column structure. Schmidt et al. (2004) demonstrated that the greater than 150-μm foram community, as determined from the individuals within specific assemblages, increases with upper water-column stratification in low latitudes in the Neogene. This shift in the size of the foram community reflects an indistinguishable combination of macroecological and macroevolutionary factors because the measure reported is affected by the relative abundance of species of different sizes as well as shifts in the extinction and/or origination of species of different sizes. Regardless, it appears that there is a shift in the size structure of marine zooplankton that follows the largest decrease in the mean size of the diatoms in the early to mid-Miocene. Currently, there is insufficient temporal resolution to determine if the trends in increasing size between the planktonic foraminifera and the diatoms are causally related. In the modern ocean, there is often an association between the size structure of the phytoplankton community, the abundance and size of organisms in higher trophic levels, and the export

of photosynthetically produced carbon into the deep sea, which increases the ocean's capacity to act as a sink for atmospheric carbon dioxide (Ryther 1969; Azam et al. 1983; Laws et al. 2000; Finkel et al. 2005). This suggests that if climate-induced environmental change in nutrient and light availability alters the size structure of marine phytoplankton and the associated marine food web, there is the potential for a climatic feedback (see Figure 1). Observation of these macroecological and macroevolutionary shifts in the size structure of the plankton lead to the question: what effect did these changes have on the evolution of marine food web structure and function over the Cenozoic?

D. The Evolution of the Modern Marine Food Web

Size-structured food webs can emerge when selection acts from the bottom-up (Loeuille and Loreau 2005). Increases in inorganic nutrient input result in evolutionary increases in organism size, total community biomass, and maximum trophic height, consistent with patterns observed in

marine systems (Bambach 1993). Furthermore, Loeuille and Loreau (2005) identify that prey size range and exploitation competition are key factors that can drive the evolution of many food web characteristics. As the variance in body sizes that can be consumed decreases, only species that are the correct size to eat specific prey evolve, resulting in simple food chains. Exploitation competition acts to decrease the fitness of individuals of similar body size and is critical for the development of diversity (Loeuille and Loreau 2005). In contrast, Stanley's cropping hypothesis advocates that the introduction of consumers to "crop" abundant phytoplankton assemblages is required to catalyze the diversification of predators and prey, and likely stimulated the explosion in metazoan diversity in the Cambrian (Stanley 1973a). Further extending the cropping hypothesis, Butterfield proposed the evolution of herbivorous meso-zooplankton, which could transfer primary production from small photoautotrophs to larger animals, was key to the diversification of the metazoans in the Early Cambrian (Butterfield 1997, 2001a, b).

The end of the Cretaceous marks one of the largest mass extinction events of the Phanerozoic, providing an opportunity to examine the coincident re-establishment of the marine food web and size structure of the plankton. In the marine environment, an estimated ~50% of genera went extinct (Sepkoski 1984). The calcareous plankton were seriously affected; only 9 of the 131 late Maastrichtian species survived (Bown et al 2004). The extinction event corresponded with the collapse of the export flux of organic carbon to the deep sea, which took several million years to recover (D'Hondt et al 1998). D'Hondt proposed that primary production likely recovered quickly, but without established assemblages of zooplankton consumers most of the primary production was recycled through the microbial food web. The recovery of primary and secondary consumers was likely required to re-establish the carbon flux to

the deep sea (D'Hondt et al 1998; D'Hondt 2005). This suggests that food supply to the benthos would have been seriously limited for several million years, a conclusion that is hard to reconcile with the timing and level of diversification of the deep-sea benthic foraminifera in the Early Cenozoic (Miller et al 1992).

The fossil record of the dominant extant herbaceous zooplankton such as the crustaceans, the copepods, euphausiids, amphipods, and decapods is extremely poor, and there is no fossil record of the planktonic urochordates, salps, and appendicularians (Rigby and Milsom 2000), making it extremely difficult to reconstruct the detailed evolution of the planktonic marine food web over the Cenozoic. Many of the groups associated with the microbial food web (heterotrophic bacteria, flagellates, and ciliates) would likely not have been seriously affected by the end-Cretaceous mass extinction or would have recovered quickly due to their inherently high rates of reproduction (Sherr and Sherr 1994). Some moderately large species of phytoplankton were present in the early Cenozoic (Finkel et al 2005), but many groups, including the planktonic forams and many metazoans, were much reduced in diversity, and many of the surviving species were small (Rigby and Milsom 2000; Gallagher 2003; D'Hondt 2005). It is probable that the larger organisms, due to their inherently slower reproductive rates and higher minimum resource requirements, took much longer to recover from the mass extinction event. The coincident recovery of the deep-sea carbon flux, the size of the planktonic forams, and the increase in fish teeth accumulation suggest a partial recovery of the planktonic marine food web that likely included the establishment of large phytoplankton or large grazing zooplankton, approximately 62 Ma (D'Hondt 2005).

Based on the diversity of the fossil records of the major eukaryotic phytoplankton groups, there was a significant change in the taxonomic structure of the marine

phytoplankton community in response to changes in climate (Falkowski *et al* 2004; Katz *et al.* 2004; de Vargas *et al.,* Chapter 12; Kooistra *et al* , Chapter 11, this volume). The calcareous nannoplankton and organic-walled cyst-forming dinoflagellates diversified through much of the Mesozoic but then declined through the Cenozoic as the diversity of the diatoms rose (Harwood and Nikolaev 1995; MacRae *et al.* 1996; Bown *et al* 2004) The diatoms have a number of unique eco-physiological abilities relative to the other major phytoplankton groups; they have an outer wall of opaline silica, they can take up large amounts of nutrients very quickly, and they store inorganic nutrients in vacuoles (Raven 1987, 1997; Stolte and Riegman 1995; Lomas and Gilbert 2000) that they can use to maintain high rates of growth when ambient concentrations of nutrients are temporarily low (Grover 1991) In addition, at a given size, diatoms have the fastest maximum growth rates of all the phytoplankton groups (Langdon 1988; Tang 1995; Raven *et al* 2006). The unique eco-physiology of the diatoms represents a new innovation for unicellular photoautotrophs to take advantage of temporal nutrient variability at certain frequencies that may have been increasingly important as the equator-to-pole temperature gradient increased through the Cenozoic (Finkel *et al* 2005). Assuming that the changes in fossil diversity reflect a change in abundance, the diatoms become an increasingly dominant part of the phytoplankton community through the Cenozoic.

The establishment of the diatoms altered the food resources available to the planktonic primary consumers and likely affected the evolution of the copepods, isopods, and appendicularians, which in turn likely affected the evolutionary establishment of particular species in the upper trophic levels. As prey, the diatoms are particularly suited to zooplankton species that are large enough to ingest them whole or break their opaline frustule (Hamm *et al* 2003; Hamm and Smetacek, Chapter 14, this volume). It is interesting to note that many copepods have mandibles lined with teeth reinforced with silica, indicating co-evolution with diatoms (Hamm *et al* 2003; Hamm and Smetacek, Chapter 14, this volume). An increase in biomass and the size of secondary and higher consumers would also have contributed to an increase in the transfer of resources to the benthos, because larger predators tend to have larger fecal pellets with a higher sinking flux (Uye and Kaname 1994; Taguchi and Saino 1998). In addition, because diatoms are often large and heavy and tend to aggregate, the dominance of phytoplankton community by diatoms may have led to an increase in the export of primary production to the deep sea, providing increased resources to the benthic community and likely contributing to their documented increases in abundance, biomass, and size through the Cenozoic (Bambach 1993)

In general, the diversity of prey is linearly related to the diversity of predators (Rosenzweig 1995), and larger prey are often associated with larger predators (Cohen *et al* 2003). A phytoplankton species that can decrease its size below the threshold of its main consumers would have both an increase in its metabolic rate and a decrease in mortality through grazing. A limitation to this diversification may be imposed by nonscalable cellular components associated with photoautotrophy that set the theoretical minimum cell size to ~1 μm (Raven 1994; Raven *et al* 2006). Once consumer species evolved to consume these smallest phytoplankton species, this downward selection pressure should somewhat dissipate. As an alternative strategy, a phytoplankter can increase its size above the threshold of its main consumer, but this has a trade-off in growth rate, efficiency of light absorption (per mass of pigment) (Finkel 2001; Finkel *et al.* 2004), and rates of nutrient diffusion and sinking (Pasciak and Gavis 1974; Gavis 1976) Larger zooplankton will also have a decreased metabolic rate; if the increase in size is more costly to the prey than the predator, then the upward size trend will cease.

Some taxonomic groups have evolved strategies to effectively increase their physical size (as experienced by their consumers) with a minimum decrease in metabolic rate. For example, many diatom species have large silica spines or other appendages and can form large chains. Diatom species are known to have nutrient storage vacuoles (Sicko-Goad et al. 1984; Raven 1987, 1997), silica spines and other appendages, and the ability to form chains, all of which allow them to increase their effective size to avoid predation but mitigate the negative effects of increased cell size on growth and sinking rates. From this perspective, the evolutionary trajectory in the size of phytoplankton species may be a consequence of an evolutionary arms race with its predators (Dawkins and Krebs 1979; Smetacek, 2001; Smetacek et al. 2004). For example, some armored heterotrophic dinoflagellates use a large pseudopodial feeding veil that permits them to extracellularly digest their prey and therefore feed on diatoms chains that can be considerably larger than themselves (Gaines and Taylor 1984; Sherr and Sherr 1994; Hamm and Smetacek this volume). The evolution of some larger diatom species through the Cenozoic (even though median frustule size decreased) does correspond with a change in the size of the larger planktonic forams (Schmidt et al 2004); these trends in increasing size between predators and prey may be causally related or due to response to the same environmental variables (Bengtson 2002). Interpretation of macroevolutionary and microevolutionary trajectories in the size of organisms is further complicated by factors such as the existence of multiple extant predators at different trophic levels with the ability to consume prey of a variety of sizes, omnivory and mixotrophy, competition for (and recycling of) inorganic and organic nutrients by heterotrophic and photosynthetic organisms, and mortality caused by parasitoids and viruses (Litchman, Chapter 16, this volume).

Phytoplankton interact and affect climate through the uptake of inorganic materials, the output of oxygen, and the production of reduced carbon compounds that form the base of the food web. The fate of photosynthetically reduced carbon is determined largely by the consumers in the food web. The size structure of the phytoplankton likely contributes to the size of the zooplankton predators, and in turn they affect the size structure of the higher trophic levels on both ecological and evolutionary time scales. The fossil record documents biotic responses to a large range of climate conditions, including the size of the organisms present. Further application of the general relationships that exist among environmental conditions, organism size and physiology, ecology, and evolution may provide additional information for the potential for feedbacks between climate and biota (see Figure 1). Continued investigation through experiments, field observation, analysis and simulation, and the development of theory will likely yield further insights into the generality and basis of the relationships between organism size and metabolic rate, abundance, diversity, and food web structure.

Acknowledgments

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