



## Novel interactions between phytoplankton and microzooplankton: their influence on the coupling between growth and grazing rates in the sea

Suzanne Strom

*Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Rd., Anacortes, WA 98221, U.S.A.*

*Tel: 360-293-2188. E-mail: stroms@cc.wvu.edu*

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### Abstract

Understanding the processes that regulate phytoplankton biomass and growth rate remains one of the central issues for biological oceanography. While the role of resources in phytoplankton regulation ('bottom up' control) has been explored extensively, the role of grazing ('top down' control) is less well understood. This paper seeks to apply the approach pioneered by Frost and others, i.e. exploring consequences of individual grazer behavior for whole ecosystems, to questions about microzooplankton–phytoplankton interactions. Given the diversity and paucity of phytoplankton prey in much of the sea, there should be strong pressure for microzooplankton, the primary grazers of most phytoplankton, to evolve strategies that maximize prey encounter and utilization while allowing for survival in times of scarcity. These strategies include higher grazing rates on faster-growing phytoplankton cells, the direct use of light for enhancement of protist digestion rates, nutritional plasticity, rapid population growth combined with formation of resting stages, and defenses against predatory zooplankton. Most of these phenomena should increase community-level coupling (i.e. the degree of instantaneous and time-dependent similarity) between rates of phytoplankton growth and microzooplankton grazing, tending to stabilize planktonic ecosystems. Conversely, phytoplankton, whose mortality in the sea is overwhelmingly due to microzooplankton grazing, should experience strong pressure to evolve grazing resistance. Strategies may include chemical, morphological, and 'nutrient deficit' defenses. Successful deployment of these defenses should lead to uncoupling between rates of phytoplankton growth and microzooplankton grazing, promoting instability in ecosystem structure. Understanding the comparative ecosystem dynamics of various ocean regions will require an appreciation of how protist grazer behavior and physiology influence the coupling between rates of phytoplankton growth and microzooplankton grazing.

### Overview

The evolution of thought on the regulation of phytoplankton communities forms an important part of biological oceanographic history. While a few prescient thinkers have always espoused a holistic view of phytoplankton regulation (Riley, 1946; Harvey et al., 1935; Johannes, 1964; Pomeroy, 1974), much early work framed problems of phytoplankton species succession and biomass change solely in terms of resource availability and competitive interaction (i.e. 'bottom up' factors). The view that grazing (a 'top down' factor) contributes equally to observed phytoplankton community composition and size has only

slowly emerged, and the consequences of this interplay between bottom-up and top-down regulation are still not always readily appreciated.

Bruce Frost's research has contributed much to the recognition of grazing as a process structuring phytoplankton communities. His work with copepods elucidated the predictable nature of these animals' feeding response to changing phytoplankton cell size and concentration (Frost, 1972, 1975). Such feeding responses were quickly explored from a theoretical viewpoint with colleagues including Lam and Steele (Lam & Frost, 1976; Steele & Frost, 1977). These papers and others from the same time period (Frost, 1980) clearly demonstrated the potential for

suspension-feeding copepods to regulate important aspects of phytoplankton communities, including size structure, overall biomass, and cell division rate (through grazer nutrient excretion). The relationship between phytoplankton and grazer capabilities, and the consequent impact on phytoplankton community dynamics, have since been used by Frost to illuminate some of the major present-day problems in ocean plankton ecology. A particular focus has been the role of grazing and its interaction with resource availability in structuring the food webs of high nitrate–low chlorophyll (HNLC) regions (Frost, 1987, 1991, 1993; Frost & Franzen, 1992; Loukos et al., 1997; Strom et al., 2000).

In the spirit of the March 2001 symposium honoring Frost's contributions to plankton ecology, my intent in this paper is to explore the influence of microzooplankton (phagotrophs <200  $\mu\text{m}$  in size) on phytoplankton communities. While Frost's early experimental and theoretical work focused on copepods, the 'microbial revolution' that has swept biological oceanography since the early 1980s has indicated that microzooplankton, primarily protists, are the major grazers of phytoplankton at most times throughout much of the world's oceans (e.g. Burkill et al., 1993; Verity et al., 1993; Landry et al., 1997; Neuer & Cowles, 1994; Sherr & Sherr, submitted). Furthermore, it is now widely recognized that the fate of most phytoplankton cells produced in the sea is to be eaten (Banse, 1992). This makes microzooplankton grazing a key process for the structuring of phytoplankton community composition, biomass, and activity, in precisely the conceptual sense envisioned by Frost and others.

Phytoplankton cell division rates (i.e. the potential for phytoplankton cells to accumulate) and rates of protist grazing can be either coupled or uncoupled in time. The nature and extent of this coupling, in concert with other loss processes such as cell sinking, viral lysis, or advection, dictate the temporal evolution of the phytoplankton community. This view relates directly to the widely employed 'Frost equations' for estimating grazing rates (specifically the coefficients of phytoplankton growth ( $k$ ) and zooplankton grazing ( $g$ ) therein) as well as to their first cousin, the dilution method of Landry and Hassett, which estimates analogous coefficients of growth and microzooplankton grazing for natural communities (Frost, 1972; Landry & Hassett, 1982). What are the attributes of protists, as grazers, that influence coupling between phytoplankton growth rates and grazing? What are

corresponding elements of phytoplankton morphology and physiology that influence the same? Because the study of planktonic protist grazers is in its infancy, there are a number of exciting and largely unexplored research areas germane to these questions. A central goal of this paper is to illustrate the potential importance of this research area, and by doing so to stimulate inquiry into this little-known yet fascinating sector of plankton ecology.

#### *Coupling between phytoplankton growth and microzooplankton grazing*

Rates of phytoplankton growth (as intrinsic growth, or cell division rates) and microzooplankton grazing may be coupled in both an instantaneous and a time-varying sense. In the instantaneous sense, a coupled system is one in which cell- or biomass-specific rates of growth and grazing are similar in magnitude; in highly coupled systems, rates might be equal. If equality persists over time and other accumulation or loss processes are inconsequential, phytoplankton biomass will remain constant, although phytoplankton production might be quite high. This situation is thought to characterize the open subarctic Pacific, and perhaps other HNLC regions (Miller, 1993; Landry et al., 1997). Conversely, in an uncoupled system, growth and grazing rates differ substantially, and large changes in phytoplankton standing stocks (e.g. blooms or precipitous declines) are likely to ensue. Temperate coastal waters represent this contrasting scenario, at least seasonally. The extent to which growth and grazing are coupled in time affects the net response of the phytoplankton community to perturbations, such as events that change light or nutrient availability, which in turn alter the phytoplankton growth rate. In a stable ecosystem, perturbations either initiate little change (high system resistance) and/or the changes that arise are short-lived (high system resilience sensu Pimm, 1984 and May, 2001). Phenomena that couple growth and grazing rates promote planktonic ecosystem stability because event-driven changes in growth rate, which might otherwise lead to changes in phytoplankton biomass and composition, are buffered by corresponding changes in grazing. It is important to note that phytoplankton biomass-specific grazing rates are dependent on both the feeding rates of individual grazers, and on grazer community biomass.

In the remainder of the paper, I first explore features of protist grazer behavior and physiology that have the potential to couple phytoplankton growth and

protist grazing. These features involve both individual (per capita) grazing rate regulation, and regulation of grazer population size. Second I describe a related set of phytoplankton features that, in concert with protist responses, could uncouple rates of phytoplankton growth and protist grazing. Throughout, the reader's attention is directed to unanswered questions and outstanding research directions related to protist grazers and their interaction with phytoplankton.

### Mechanisms promoting coupling: the grazer imperative

#### *Higher grazing rates on faster-growing cells*

A direct and potentially powerful coupling of phytoplankton growth and microzooplankton grazing would occur if microzooplankton grazed at higher rates on faster-growing prey cells. There is evidence for such a relationship in the protist bacterivory literature, in that bacterivorous flagellates tend to feed at higher rates on faster-growing bacteria (Gonzalez et al., 1993; del Giorgio et al., 1996). This has been explained as a response to the larger size of those bacterial cells, which are captured more efficiently by some protist grazers (Andersson et al., 1986; Gonzalez et al., 1990). On the other hand, some nanoflagellates are capable of ingesting even submicron-sized colloids and viruses, albeit inefficiently (Gonzalez & Suttle, 1993; Tranvik et al., 1993; Gonzalez, 1996). Given the range of protist species and grazing capabilities present in a typical plankton sample, the effectiveness of prey cell size in linking growth rates with predation is not yet clear.

Data from field dilution experiments often demonstrate that phytoplankton growth and microzooplankton grazing rates are positively correlated. For example, accessory pigment analysis has shown that, within a given community during a single experiment, the fastest-growing phytoplankton taxa often experience the highest grazing rates (Fig. 1, see also Burkill et al., 1987; Strom & Welschmeyer, 1991; McManus & Ederington-Cantrell, 1992; Verity et al., 1996). The source of these positive correlations is unknown. In some cases, the fastest-growing taxa are not the most abundant, so increased per capita feeding rates in response to increased abundance (as predicted by laboratory-generated functional response curves) cannot fully explain the correlations. Micrograzer communities contain a mixture of flagellate and ciliate taxa with different grazing capabilities, and these taxa are

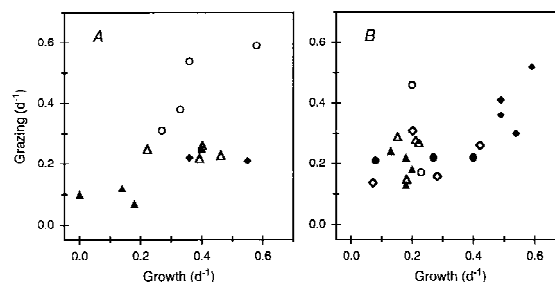


Figure 1. Comparative rates of phytoplankton growth and microzooplankton grazing for individual phytoplankton taxa, based on changes in accessory pigment concentration (indicative of taxon) during seawater dilution experiments. Note broad positive correlations between rates of growth and grazing. Experiments conducted during (A) June and (B) September 1987 at subarctic Pacific Station P (50° N, 145° W). Data from Strom & Welschmeyer (1991). Pigments: chlorophyll *b* (filled circles); chlorophyll *c*<sub>3</sub> (open circles); peridinin (open diamonds); zeaxanthin (filled diamonds); 19'-butanoyloxyfucoxanthin (open triangles); 19'-hexanoyloxyfucoxanthin (filled triangles). Diatom accessory pigments fucoxanthin and diadinoxanthin excluded from analysis.

quite plastic in their own growth rates (see below). Increased production (yielding increased biomass) of a grazer population, in response to high production of fast-growing prey, would result in the relationship described above; such a relationship is indicated by the strong correlations between microzooplankton biomass and community grazing rates found during the second iron fertilization experiment (Landry et al., 2000). The possibility that differential growth of microzooplankton across the dilution series contributes artifactually to observations of coupled growth and grazing rates (Dolan et al., 2000) must also be considered.

In addition to community-level responses, an increase in grazing rates at the individual level could contribute to higher grazing on fast-growing cells. Such an increase could arise from shifts in prey preference or from acceleration of individual feeding activity, and might occur in response to increases in prey population size (see above, however) or nutritional value (e.g. nitrogen content, Goldman et al., 1979) of faster-growing prey cells. Studies investigating the relationship between grazing rates or prey preferences of individual protists and growth rates of their phytoplankton prey are rare to non-existent. For copepods, higher grazing on faster-growing cells of a given phytoplankton species has been demonstrated in several studies (Cowles et al., 1988; Butler et al., 1989; Sterner & Smith, 1993). Protists are capable of sensing biochemical properties of their prey cells (e.g. Monger

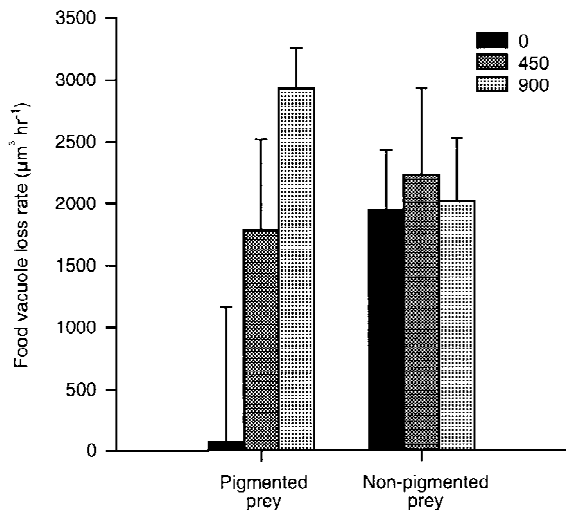


Figure 2. Rates of digestion (as average food vacuole loss rates  $\pm$  or  $-1$  s.d. measured in triplicate bottles of grazers without food over 2 d) for the heterotrophic dinoflagellate *Noctiluca scintillans* (non-bioluminescent strain) at three irradiance levels (dark, 450 and 900  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). *N. scintillans* had been pre-fed on two contrasting prey types: the tintinnid *Coxiella* sp. (a heterotrophic ciliate) and the autotrophic (pigmented) dinoflagellate *Prorocentrum micans*. Light strongly increased *N. scintillans* digestion rate when fed the pigmented prey (one-way ANOVA,  $p=0.012$ ), but had no effect on digestion rate for the non-pigmented ciliate prey (one-way ANOVA,  $p=0.814$ ). Differences between absolute rates of digestion between the two prey types (e.g. in the dark) are attributed to differences in carbon: volume ratios (i.e. the large unoccupied lorica volume of each tintinnid) and prey biochemical differences. Data from Strom (2001).

et al., 1999; Strom et al., 2001), and both ciliates and flagellates have been shown to feed preferentially on more nutritious phytoplankton species (Stoecker et al., 1986; Buskey, 1997). Protists can also demonstrably reject undesirable particles after capture (Taniguchi & Takeda, 1988; Wetherbee & Andersen, 1992; Stoecker et al., 1995) or even after ingestion (Boenigk et al., 2001a) and can 'learn' (i.e. change their behavior after exposure to a stimulus) to avoid unpalatable materials (Tarran, 1991; Boenigk et al., 2001b). Thus feeding variation based on differences in phytoplankton growth rate seems within the behavioral capabilities of these grazers.

#### Light-aided digestion

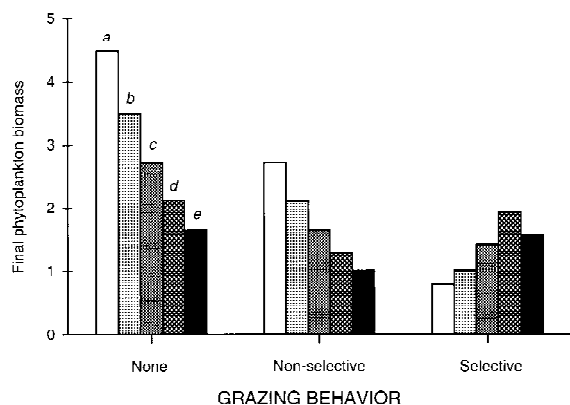
Recent work (Strom, 2001) has shown that some strictly heterotrophic protists digest phytoplankton at a higher rate in the light than in the dark (Fig. 2). Furthermore, these light-dependent digestion differences appear to translate into substantially higher

rates of protist feeding and population growth (see also Skovgaard, 1998), so that grazing potential may be linked to light intensity. Light-aided digestion in protists has been seen only for phytoplankton prey, and was not observed when prey was heterotrophic (Fig. 2). The phenomenon is mediated by visible light, which includes photosynthetically active wavelengths. These observations suggest that the digestive mechanism involves the photosynthetic apparatus of ingested prey cells. One hypothesis is that active oxygen compounds, whose formation should be promoted by photosensitization reactions involving chlorophyll (Halliwell & Gutteridge, 1989), may directly decompose lipids and proteins of the ingested phytoplankton cell once the cell is enclosed in the degradative environment of the protist food vacuole. Preliminary confirmation of this hypothesis was provided by use of dihydrorhodamine (Royall & Ischirpoulos, 1993), a compound (membrane-permeable in its non-fluorescent state, converted to a fluorescent, non-permeable compound upon reaction with active oxygen) that we found to fluoresce brightly in *Noctiluca scintillans* food vacuoles, but only when the dinoflagellate fed in the light (Zirbel & Strom, 2001).

Light-aided digestion could result in both increased rates of 'digestive throughput' (particularly when prey concentrations are high and feeding is not encounter-rate limited) and in more extensive digestive breakdown and assimilation of compounds from ingested cells (Strom, 2001). Photobiochemical degradation could be especially important for utilization of phytoplankton cells that are refractory to strictly biological digestion. Should the phenomenon prove widespread, the implications for coupling of phytoplankton growth with microzooplankton grazing in nature are great. Visible light should enhance rates of both growth and protist herbivory in the same sense, though through separate mechanisms, promoting tight coupling between the two across the myriad environmental gradients (mixing depth, time of day, season, latitude, cloud cover, water column transparency) that influence light availability. Considerable work will be necessary to establish the importance of light-aided digestion for natural microplankton communities.

#### Nutritional plasticity: selective feeding, omnivory, and mixotrophy

Studies of food vacuole contents in field-collected planktonic protists indicate that many of these grazers are dietary generalists in nature, feeding on a range



**Figure 3.** Grazing behavior profoundly influences phytoplankton community composition. Shown is biomass of five phytoplankton species (a–e) after 5 d assuming three different grazing behaviors: no grazing, non-selective, and selective grazing. Model and data from Frost (1980). Final biomass ( $P_{ti}$ ) of  $i$ th phytoplankton species (relative units) calculated from:  $P_{ti} = P_{oi} e^{(\mu_i - g_i)t}$  where  $P_{oi}$ =initial biomass (=1 for all species);  $\mu_i$ =phytoplankton growth rate (=0.30, 0.25, 0.20, 0.15, 0.10  $\text{d}^{-1}$  for species a through e, respectively);  $g_i$ =zooplankton grazing rate; and  $t$ =time (5 d). For non-selective feeding,  $g$  on all phytoplankton species was set to 0.1  $\text{d}^{-1}$ . For selective feeding,  $g_i$ =0.35, 0.25, 0.13, 0.02, and 0.01  $\text{d}^{-1}$  on species a through e, respectively.

of prey types and sizes (Bernard & Rassoulzadegan, 1993; Jacobson & Anderson, 1996). Whether and how these organisms select from the range of particle types present is, however, largely unknown. A simple model presented by Frost (1980) illustrates the potency of the selective feeding process, in concert with variations in phytoplankton growth rate, for shaping phytoplankton community structure (Fig. 3). A number of laboratory studies, most focused on bacterivory, have explored selective feeding in free-living protists (see summaries by Verity, 1991; Hansen & Calado, 1999; Strom et al., 2000), and clearly these organisms do alter their diet in response to changes in prey availability. The determinants of such dietary shifts are, however, far from clear. Do protist grazers simply feed on particles in proportion to their availability in the environment? Does grazing on rare prey types decrease disproportionately as these become less abundant (the classic definition of dietary switching sensu May, 1977; Murdoch, 1969)? Is prey selection influenced by overall prey abundance, as suggested by optimal foraging theory (Stephens & Krebs, 1986) and a single study of bacterivorous flagellates (Jürgens & DeMott, 1995)?

Clearly there will be no single selective feeding function that describes the vast diversity of planktonic protist taxa and feeding strategies. Equally clearly, prey selection and dietary breadth will be acted upon

by the environment, so that no one function will apply universally even to a given grazer species. However, it is reasonable to expect some general features that extend across taxa and environments. The importance of such information can be seen in the numerous plankton dynamics models that now incorporate omnivory, specifically formulated as dietary switching, as the mathematical formulation describing the relationship between grazing activity and prey abundance (e.g. Fasham et al., 1990; Loukos et al., 1997; Pitchford & Brindley, 1999). Without these or related formulations, the models cannot robustly reproduce temporal cycles in phytoplankton, nutrient and grazer stocks as seen in nature, and tend to predict ecosystems with a higher level of instability (Strom et al., 2000). Yet for marine microzooplankton, we do not know whether such mathematical formulations have their roots in real behaviors. In general, omnivory has long attracted the attention of theoretical ecologists for its potent ability to stabilize temporal fluctuations in prey biomass (Oaten & Murdoch, 1975; Chesson, 1983; Hutson, 1984). Considerably less attention has been paid by experimental ecologists, particularly in the realm of marine microzooplankton where fundamental aspects of feeding and growth rate potential even on single prey diets have only recently been described.

Nutritional plasticity in phagotrophic protists also encompasses mixotrophy, a strategy that is common and widespread in the ocean (reviewed by Riemann et al., 1995; Caron, 2000). Mixotrophic protists include photosynthetic flagellates that also phagocytize and digest prey, as well as ciliates and dinoflagellates that sequester chloroplasts obtained from ingested phytoplankton. The extent to which ingestion versus photosynthesis provide energy and nutrients to mixotrophs varies widely, from chloroplast-retaining species that are obligate feeders to primarily photosynthetic protists that phagocytize only rarely, perhaps as a means of obtaining scarce nutrients (Jones, 1994). Protist nutritional plasticity in general couples phytoplankton growth and microzooplankton grazing for several reasons. First, the phenomenon potentially creates a refuge for prey populations when abundances grow low, as protists have access to other prey types and energy sources. Second, mixotrophy and omnivory yield a wide range of available energy and nutrient sources for a given grazer population, potentially enhancing grazer survival in times of scarcity. Both the creation of prey refuges and enhanced grazer survival will tighten the coupling between phytoplankton and microzooplankton grazers and lead to enhanced sys-

tem stability, by reducing the magnitude of 'boom and bust' population cycles. Research utilizing mixed diets, including systematic exploration of selective feeding and multiple nutritional modes, is a crucial next step for the exploration of phytoplankton–microzooplankton relationships in the sea.

#### *Protist growth rates and resting stages*

As suggested above, adaptations that allow individual grazers to survive times of food scarcity will tend to stabilize not only grazer population sizes, but prey population sizes as well. The formation of metabolic resting stages on the part of grazers (the 'seed bank' concept) can lead to coupling between phytoplankton growth and microzooplankton grazing by ensuring that a supply of grazers is available when environmental conditions change. Some ciliate and dinoflagellate species can form extraordinarily long-lived cysts that typically deposit to the sediments (e.g. Pfiester & Anderson, 1987; Reid, 1987). Other flagellates, when starved, have been shown to enter metabolic resting stages characterized not by gross morphological changes, but by substantial reductions in respiration rate (Finlay, 1983; Caron et al., 1990). Still other protists, notably oligotrich ciliates, die rapidly when deprived of food for even 24 h (Montagnes, 1996; Jakobsen & Hansen, 1997). What sorts of resting stages characterize typical marine protist grazers, especially in oceanic waters where benthic deposition is an unlikely survival strategy? What is the time scale over which these stages enter and leave the population, and what are the environmental cues? Is the seemingly greater starvation resistance of heterotrophic flagellates, relative to ciliates, a characteristic difference between these two groups, and does it play a role in their ecological niche partitioning?

The high potential population growth rates of protist grazers (summarized by Hansen et al., 1997) are an alternative and oft-cited means for promoting coupling between the grazing capacity of these populations and the growth rates of their phytoplankton prey (e.g. Banse, 1992 and many others). The argument is that increases in phytoplankton growth rate can be matched quickly by increases in grazer growth, because heterotrophic protists have maximum population growth rates that equal or exceed those of phytoplankton. Whether such coupled responses promote ecosystem stability depends on the fate of the increased grazer production. With no transfer to higher trophic levels (i.e. carnivores), grazing is likely eventually to ex-

ceed phytoplankton growth. On the other hand, highly efficient carnivory will limit the extent to which increased grazer growth rates can lead to increased grazing capacity. As has been widely demonstrated (Stoecker & Evans, 1985; Edwards & Yool, 2000; Steele & Henderson, 1992), predatory organisms can strongly influence phytoplankton–microzooplankton interactions.

The intrinsic growth rates of protist grazers are difficult to measure in natural systems. A few studies have attempted to estimate these intrinsic growth rates through size fractionation techniques (e.g. Capriulo & Carpenter, 1980; Verity, 1986; Weisse & Scheffl-Möser, 1991); in general, the technique has been more widely applied in freshwater systems (Carrias et al., 2001 and references therein). *In situ* net growth rates of protist grazers sometimes approach temperature-limited physiological maxima. When they do not, the reasons (food quality? quantity? predation within a given size fraction? experimental artifact?) can be hard to determine. Several recent papers point to the existence of complex trophic cascades within marine microplankton communities, suggesting that top-down control of protist populations sets limits on net growth (Wikner & Hagström, 1988; Calbet et al., 2001; Dolan, 1991). However, methodological problems with size fractionation techniques abound (Landry, 1994). This seems to be an arena ripe for the application of molecular techniques coupled with flow cytometric or imaging-in-flow analysis, as has been brought to bear successfully on natural intrinsic growth rates of prokaryotes (e.g. Mann & Chisholm, 2000). How often are the theoretical high population growth rates of protist grazers ever realized as high net growth rates in the sea? If high net growth rates are not realized, is this because intrinsic growth rates are low (due, for example, to suboptimal food conditions), or because predation on these grazers exerts strong top-down control on their population sizes? In general, how important are high potential protist growth rates for coupling in natural systems?

#### *Protist defenses against their own predators*

By the same argument as made above for high population growth rates, resistance to predation on the part of microzooplankton can lead to coupling between microzooplankton and phytoplankton. A growing literature indicates that copepods are an important suite of predators on planktonic protists (Stoecker & Capuzzo, 1990; Gifford, 1993; Fessenden & Cowles, 1994;

Atkinson, 1996), although it remains to be established whether this trophic linkage is quantitatively more important than predation from within the microplankton by omnivorous or carnivorous protists (Paffenhöfer, 1998). There are interesting examples in the literature of protist grazer defenses against predators, although typically these involve benthic freshwater taxa. Wicklow (1997) and Kuhlmann et al. (1999) describe inducible morphological changes, such as formation of horns, ribs and other protrusions, produced by numerous ciliate species in the presence of predatory protists. In many cases, these protrusions have been shown to reduce predation rates. Several of these ciliate species also undergo survival-enhancing behavioral changes in the presence of predators (such as amoebae) that are not size-selective. Morphological changes and a transformation into parasitic cells that attack their own predators are induced in a tetrahymenid ciliate by predatory mosquito larvae (Washburn et al., 1988). Species of *Blepharisma*, a benthic freshwater heterotrichous ciliate, commonly produce a pink pigment (blepharismin) that can have a defensive function (Miyake et al., 1990). Kuhlmann et al. (1999) speculate that the morphological variation exhibited by many ciliate species might be related to induced defenses; almost nothing is known of such responses for marine planktonic protists.

Numerous other aspects of planktonic protist physiology and behavior might also be related to predation defense, although often these features have not been viewed as defensive, and certainly many may have multiple functions. For example, many athecate heterotrophic dinoflagellates have trichocyst-like organelles whose release is triggered by disturbance. Other heterotrophic dinoflagellates are bioluminescent, and a few studies suggest that the flashes of light generated when these cells are disturbed can deter visual predators (Buskey et al., 1983 and references therein). Some taxa of large protists have hard cell coverings, often with long protruberances, including the *Protoperidinium* spp. and related dinoflagellates (heavy cellulose theca) and tintinnid ciliates (siliceous or agglutinated lorica). For some dinoflagellates these protruberances are thought to increase flotation (Schütt 1892, cited in Taylor, 1987), but for other species the cell coverings have no demonstrable function, and in the case of tintinnids are known to actually increase sinking rate (Capriulo et al., 1982). Could they be defenses against predators, either increasing effective cell size in a manner analogous to diatom spines (Taylor, 1987), or rendering

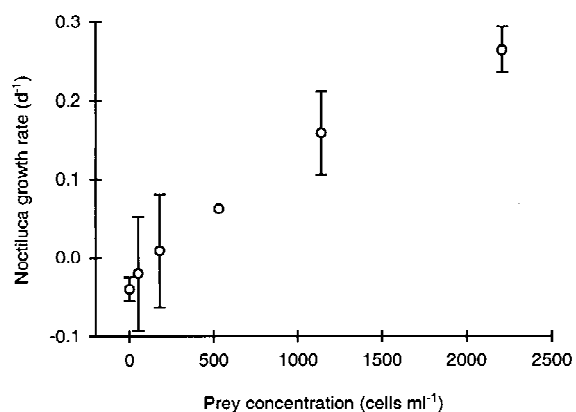


Figure 4. The heterotrophic dinoflagellate *Noctiluca scintillans* grows on the 'toxic' photosynthetic dinoflagellate *Alexandrium fundyense*. Plotted are population growth rates (average and range of observations) for *N. scintillans* (northern Puget Sound isolate) grown on *A. fundyense* (strain CCMP 1719). Rates calculated from *N. scintillans* cell densities measured at 0 and 2 d in duplicate bottles at each prey density and time point, and assuming exponential growth. (Experiment conditions: *N. scintillans* pre-starved 1 d, incubated in 62-ml polycarbonate bottles in sterile filtered seawater with *A. fundyense* grown in f/2-silicate; bottles incubated in darkness on plankton roller [ca. 2 rpm] at 15 °C. Separate bottles sampled in their entirety for each *N. scintillans* density estimate by preserving contents with acid Lugol's solution.)

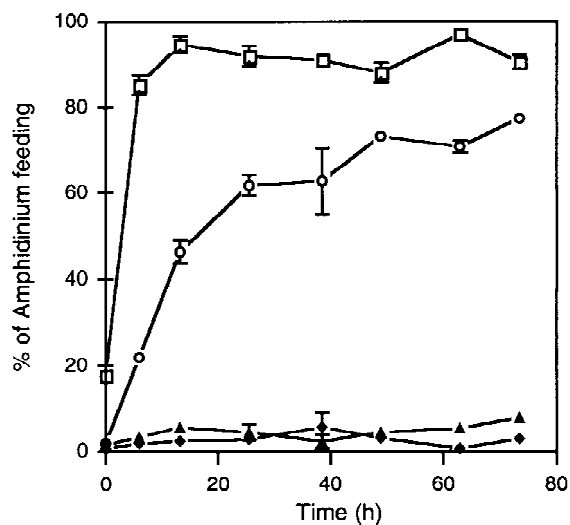


Figure 5. Responses of *Amphidinium longum* feeding activity to 4 strains of *Emiliana huxleyi* (all offered at 50 000 cells ml<sup>-1</sup> to pre-starved *A. longum*). Data points are averages of duplicate bottles, with error bars showing range of values. Open symbols: *E. huxleyi* strains with low DMSP lyase activity (circles: CCMP 370; squares: CCMP 374). Filled symbols: *E. huxleyi* strains with high DMSP lyase activity (triangles: CCMP 373; diamonds: CCMP 379). See Strom et al (submitted A) for methodological details.

the cell less palatable (DeMott, 1995)? Chemical defenses (see below) might also be synthesized de novo or sequestered from prey; some protist grazers are capable of feeding on phytoplankton species toxic to potential predators such as copepods (Fig. 4, see also Jeong & Latz, 1994; Kamiyama, 1997; Jeong et al., 1999b). Finally, swimming behavior is a potent mediator of escape. Planktonic ciliates that can 'jump' have been shown to escape more readily from copepod predation than ciliates that swim at a constant speed (Jonsson & Tiselius, 1990; Broglio et al., 2001). The dinoflagellate *Noctiluca scintillans* cannot ingest the smaller heterotrophic dinoflagellate *Oxyrrhis marina*; the latter swims actively enough to free itself from the mucous net deployed by *N. scintillans* for prey capture (pers. obs.). If 'top-down' control is an important element of population regulation for protist grazers in the sea, there would be strong evolutionary pressure for the retention of predation-resistant morphologies and behaviors. This is a research area rich with potential for future exploration.

### Mechanisms promoting uncoupling: the phytoplankton imperative

#### Chemical defenses

Although reduction of herbivory through chemical deterrence plays a fundamental role in the ecology and evolution of terrestrial and marine benthic communities (Hay & Fenical, 1988; Spencer, 1988; Tollrian & Harvell, 1999), the phenomenon of chemical defense has received much less attention from marine plankton ecologists (Wolfe, 2000). Chemical defense strategies have the potential to reduce coupling between phytoplankton and their grazers by several means: by reducing grazer population sizes through acute mortality (i.e. lethal defenses) or reductions in grazer productivity (i.e. defenses that cause physiological impairment); and by reducing feeding rates of individual consumers (i.e. sublethal defenses that affect prey palatability). Several instances of lethal phytoplankton defenses against protist grazers have been described, all involving harmful bloom-forming phytoplankton taxa (reviewed by Turner & Tester, 1997), although it should be noted that some protists feed and grow on 'toxic' phytoplankton with impunity (e.g. Jeong et al., 1999a,b). Indeed, formation of harmful phytoplankton blooms must involve the suppression of grazing

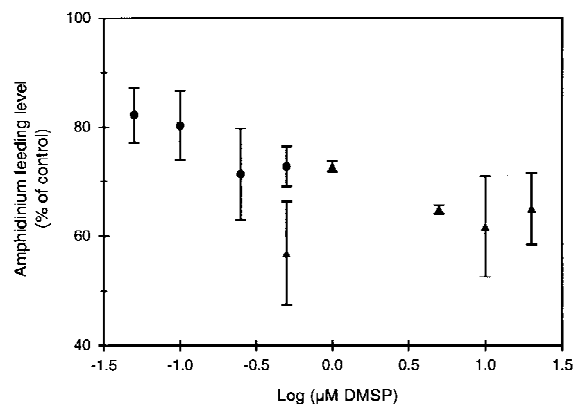


Figure 6. Inhibition of feeding in *Amphidinium longum* over a range of DMSP addition levels. Feeding data as fraction of population with ingested *Emiliania huxleyi* (strain CCMP 374) normalized to control (no DMSP addition) feeding levels. Data points show average of replicate measurements  $\pm 1$  SD. Circles: experiment JC-2 ( $n=3$ ); triangles: experiment SEL-6 ( $n=2$ ). See Strom et al. (submitted B) for methodological details.

(Smayda, 1997), and is an expression of ecosystem instability inasmuch as it indicates low resilience.

While lethal effects of phytoplankton can be dramatic, most marine phytoplankton species are not known to kill protist grazers. Potentially more widespread within the plankton are sublethal chemical defenses, compounds that either impair grazer activity without killing the grazers, or that chemically signal, 'Don't feed on me'. Free-living protist grazers are demonstrably capable of responding to prey cell surface properties (see above) as well as dissolved cues (Spero, 1985; Sibbald et al., 1987; Strom & Buskey, 1993; see Wolfe, 2000 for other examples). Furthermore, Boenigk et al. (2001a,b) have recently shown that undesirable particle types can be egested shortly after ingestion. We have been exploring the production and breakdown of dimethylsulfoniopropionate (DMSP) as a possible sublethal chemical defense system.

Numerous phytoplankton species, particularly dinoflagellates and haptophytes but others as well, produce DMSP (Keller, 1988/1989; Keller et al., 1989). Some of these taxa, including *Phaeocystis* spp. and *Emiliania huxleyi*, are not known to be toxic but do tend to form persistent blooms indicative of grazing suppression. DMSP is cleaved into dimethylsulfide (DMS) and acrylate by the constitutive phytoplankton enzyme DMSP lyase (Steinke et al., 1998), and DMSP cleavage is activated by cell lysis and other stressors, including grazing (Wolfe & Steinke, 1996; Wolfe et al., in press). Nearly all of the protist grazers



investigated to date feed at higher rates on strains of *E. huxleyi* with low DMSP lyase activity (Strom et al., submitted-a); in extreme cases, high-lyase *E. huxleyi* strains are avoided entirely, even in the absence of alternate prey (Fig. 5). Curiously, it is not the products of DMSP cleavage that elicit this response. Protists showed no change in grazing rate when exposed to DMS or acrylate (Strom et al., submitted-b); rather, DMSP itself caused reductions in feeding ranging from 13 to nearly 100% relative to control rates in 4 tested grazer species. For the heterotrophic dinoflagellate *Amphidinium longum*, feeding reductions were proportional to added DMSP concentration (Fig. 6). The relationship between high DMSP lyase activity on the part of some *E. huxleyi* strains and DMSP-induced feeding reductions is not yet clear. However, this sublethal chemical defense system and others like it could, through effects on phytoplankton–protist grazer coupling, profoundly influence phytoplankton community structure and evolution in the sea.

### Morphological defenses

Size alone sets limits on the availability of phytoplankton to grazers. Each grazer has upper and lower limits on the particle size that can be captured and ingested (Fenchel, 1987). These limits change, however, as protist grazer morphology and feeding behavior adjust in response to available prey (Calado et al., 1998; Goldman & Dennett, 1990). Furthermore, as a community, protist grazers can feed on a wide particle size spectrum, with dinoflagellates typically targeting relatively large and ciliates and nanoflagellates relatively small particles (Hansen et al., 1994). Although phytoplankton morphologies such as spines and horns, in that they effectively increase prey cell size, are often assumed to have a defensive function, there are few if any data supporting the efficacy of such defenses against protists on the whole-community level. Again, somewhat more is known for freshwater systems. Van Donk et al. (1999) summarize a fascinating body of evidence for chemically triggered changes in freshwater phytoplankton morphology: ‘kairomones’ released by feeding *Daphnia* spp. induce colony formation and spine elongation in several chlorophyte species, rendering them less susceptible to small crustacean grazers. Another intriguing hypothesis is that heavily silicified diatoms such as *Fragilariopsis kerguelensis*, an antarctic marine species, have evolved their thick siliceous frustules as a defense against grazers (Verity & Smetacek, 1996). There are currently no

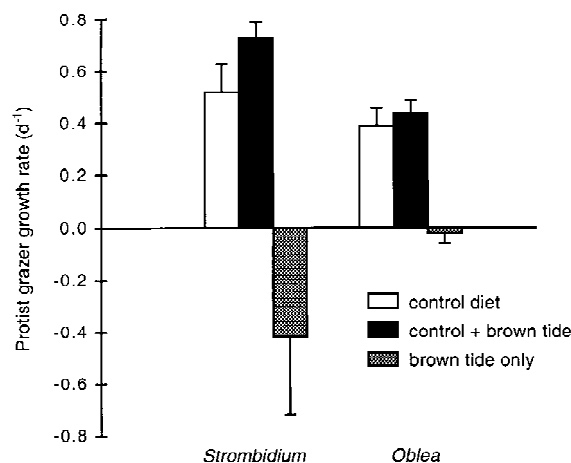


Figure 7. Growth rates of two heterotrophic protists on control diets, Texas ‘brown tide’ *Aureoumbra lagunensis*, and a mixture of control and brown tide diets. Growth was not inhibited by the presence of brown tide as long as control phytoplankton species were available. Total phytoplankton concentration was the same ( $750 \mu gC l^{-1}$ ) in all treatments, equally partitioned among the available food species. Control diets: *Emiliana huxleyi*+*Isochrysis galbana* for small ciliate *Strombidium* sp.; *Dunaliella tertiolecta*+*Isochrysis galbana* for small heterotrophic dinoflagellate *Oblea rotunda*. Control diet species grown in f/2-silicate; brown tide collected from Laguna Madre 1 d prior to experiments, prescreened through  $20 \mu m$  Nitex mesh, salinity adjusted to 30 psu with distilled water, and stored at  $20^{\circ}C$ . Experiments conducted in sterile filtered ( $0.2 \mu m$ ) 30 psu seawater in triplicate 60-ml polycarbonate bottles (dim light,  $20^{\circ}C$ ). Growth rates calculated from acid Lugol’s-preserved samples taken initially and after 3 d incubation assuming exponential growth.

data available with which to evaluate this hypotheses, although *F. kerguelensis* was one of the dominant species in the bloom that resulted from the recent Southern Ocean iron fertilization experiment (Gall et al., 2001), and morphological grazing resistance was invoked in explaining the remarkable persistence of this bloom (Boyd, in press). We know that some dinoflagellate species can feed on even very large diatom cells using pallium or peduncle (Hansen & Calado, 1999). Demonstrating that size and silicification are effective defenses against planktonic protist grazers awaits appropriate experimentation.

### Nutritional inadequacy

Nutritional inadequacy, in which a phytoplankton species lacks compounds essential for grazer growth or reproduction, could in some cases promote uncoupling between phytoplankton and their microzooplankton grazers. This phenomenon may be most effective during blooms, when a single phytoplankton species

dominates the community and other, potentially more nutritious species are not widely available. Nutritional inadequacy is not easy to distinguish from sublethal toxicity (Jonasdottir et al., 1998) and, although the two mechanisms can both lead to uncoupling in the sense described here, there are numerous differences in their implications for plankton food web dynamics. No grazer species, obviously, grows equally well on all ingestible foods (e.g. Droop, 1966; Verity & Villareal, 1986; Strom & Morello, 1998). Whether nutritional inadequacy ever translates into a competitive edge for a phytoplankton species in nature is less clear. There is some evidence that this may be the case for Texas 'brown tide' organism *Aureoanra lagunensis*, a persistent, bloom-forming pelagophyte. A ciliate and a heterotrophic dinoflagellate fed *A. lagunensis* in combination with a high quality control diet experienced no deleterious effects, but the same grazers were unable to grow on *A. lagunensis* alone (Fig. 7). Other data suggest that growth responses to *A. lagunensis* are species-specific, some protists growing well on a pure brown tide diet and others exhibiting depressed growth (suggestive of toxicity) even in dietary mixtures (Buskey & Hyatt, 1995). Brown tide cells also produce a mucous coating, particularly in stationary phase and at very high salinities, which has been hypothesized to interfere with protist grazing (Liu & Buskey, 2000). Much laboratory investigation of protist grazers has been done using diets optimized for continued survival and growth in culture. How the presence of nutritionally inadequate phytoplankton influences feeding selectivity and grazer growth, and whether such influences are important in natural communities, remain to be established.

### Summary

The marine planktonic realm is typically one of great sparseness, high diversity, and patchy distribution: a dilute and ephemeral feeding environment for protist grazers. At the same time, nearly all phytoplankton produced in this environment are consumed, primarily by microzooplankton. While recognizing the myriad other environmental features influencing phyto- and microzooplankton (Margalef, 1978), these conditions create a scenario for strong selective pressure in an evolutionary sense. For protists, adaptations that maximize prey encounter and utilization while allowing for survival in times of scarcity should predominate in the community. As detailed above, such adaptations

tend to increase the coupling between phytoplankton growth and microzooplankton grazing rates, adding stability (i.e. resilience and resistance sensu Pimm, 1984) on an ecosystem level. Indeed, the lower trophic levels of many marine planktonic ecosystems are notable for their high degree of stability (Walsh, 1976; Venrick et al., 1987; Miller et al., 1991). The high level of grazing pressure sustained by most marine phytoplankton communities should also promote intense selection, in this case for grazing resistance. Such adaptations uncouple phytoplankton growth and grazing loss, and tend to increase the temporal variability of the ecosystem. Phenomena such as episodic bloom formation and demise, characteristic of some ocean regions (Longhurst, 1998), can be viewed as a manifestation of such uncoupling, and explanations for such instabilities should be sought, in part, in the relationships between phytoplankton and their grazers. A view of the world that incorporates the capabilities and adaptations of individual organisms, particularly as they influence the interplay between growth and grazing processes, will be essential for further discovery of the fundamentals that govern planktonic ecosystems.

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