J. Eukaryot. Microbiol., 51(2), 2004 pp. 156–168

Interactions between Planktonic Microalgae and Protozoan Grazers[1]

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ABSTRACT. For an algal bloom to develop, the growth rate of the bloom-forming species must exceed the sum of all loss processes. Among these loss processes, grazing is generally believed to be one of the more important factors. Based on numerous field studies, it is now recognized that microzooplankton are dominant consumers of phytoplankton in both open ocean and coastal waters. Heterotrophic protists, a major component of microzooplankton communities, constitute a vast complex of diverse feeding strategies and behavior which allow them access to even the larger phytoplankton species. A number of laboratory studies have shown the capability of different protistan species to feed and grow on bloom-forming algal species. Because of short generation times, their ability for fast reaction to short-term variation in food conditions enables phagotrophic protists to fulfill the function of a heterotrophic buffer, which might balance the flow of matter in case of phytoplankton blooms. The importance of grazing as a control of microalgae becomes most apparent by its failure; if community grazing controls initial stages of bloom development, there simply is no bloom. However, if a certain algal species is difficult to graze, e.g. due to specific defense mechanisms, reduced grazing pressure will certainly favor bloom development. The present contribution will provide a general overview on the interactions between planktonic microalgae and protozoan grazers with special emphasis on species-specific interactions and algal defense strategies against protozoan grazers.

Key Words. Bloom control, defense mechanisms, grazing, interaction, microalgae, protozoa.

IN the past years, there has been a growing appreciation that microzooplankton are the major consumers of phytoplankton production in the sea. Microzooplankton, generally defined by size (20–200 μm, Sieburth, Smetacek, and Lenz 1978), are abundant and important grazers in such contrasting environments as the eutrophic, shallow, and highly turbid coastal Wadden Sea (Tillmann and Hesse 1998) and the oligotrophic Eastern tropical Pacific (Beers and Stewart 1971), or the Mediterranean (Gomez and Gorsky 2003) and polar (Archer et al. 1996; Levinsen and Nielsen 2002) coastal areas. Systematically, the microzooplankton include a large number of developmental stages of many pelagic and benthic animals, very few adult metazoans, and a wide range of protozoa. Because of their often dominant role within the microzooplankton, the present paper will focus on the role of protozoa in microalgae bloom dynamics. To explicitly include the large and growing number of phagotrophic mixotrophs within the protozoa, the term micrograzers seems to be more appropriate and will be used synonymously with protozooplankton in the following discussion.

Herbivorous protistan grazers are ubiquitous and abundant in the sea and are diverse not only in terms of taxonomy, but also in terms of size and feeding behavior. The protozooplankton contain representatives of all free-living protozoan taxa, i.e. the ciliates, flagellates, and sarcodines (see e.g. Laybourn-Parry 1992). Heterotrophic protists constitute a vast complex of diverse feeding strategies and behaviors that allow them access to even the larger phytoplankton species. Several papers report high numbers of protistan species during bloom events, indicating that microplankton grazing may substantially contribute to the decline of high microalgal biomass. This assumption is supported by laboratory studies showing the capability of different protistan species to feed and grow on bloom-forming algal species. Because of short generation times, phagotrophic protists can react rapidly to short-term variation in food conditions and thus fulfill the function of a heterotrophic buffer, that might balance the flow of matter in case of rapid phytoplankton growth. The importance of grazing as a control of microalgae becomes most apparent through the failure of bloom formation; if community grazing controls initial stages of bloom development, there simply is no bloom. However, if a certain algal species is difficult to graze, e.g. due to specific defense mechanisms, reduced grazing pressure will certainly favor bloom development.

Feeding strategies and food spectrum. Phagotrophic dinoflagellates are known to feed by a variety of mechanisms (reviewed by Elbrächter 1991; Hansen 1998; Hansen and Calado 1999; Schnepf and Elbrächter 1992). Direct engulfment of whole prey is widespread and occurs in many naked dinoflagellate genera, but there are also a few fully thecate species for which engulfment of intact prey organisms has been described (Biecheler 1952; Jeong et al. 1999b; Skovgaard 1996a). Among heterotrophic thecate dinoflagellates, pallium feeding is common. The prey is surrounded by a pseudopodium, the pallium, originating from the flagella pore, and digestion takes place outside the main cell body (Jacobson and Anderson 1986). Another group of dinoflagellates uses a feeding tube to suck the contents of their prey, with two different types of feeding tubes (peduncle and phagopod) having been described (see Hansen and Calado 1999).

Prey reported to be used by dinoflagellates include almost all kind of particles present in the ocean from bacteria, nanoflagellates, microalgae, and microzooplankton to eggs of copepods, marine snow, and injured metazoans (Jeong 1999). However, the capability of a given dinoflagellate species to feed and grow on certain prey types is dependant on a number of factors, including size, chemoattraction, and swimming behavior of the prey (e.g. Buskey 1997; Hansen 1992; Tillmann and Reckermann 2002). Predator:prey size ratios reported for athecate dinoflagellates (Hansen 1992; Jakobsen and Hansen 1997; Naustvoll 2000b) as well as thecate dinoflagellates (Naustvoll 2000a) show that phagotrophic dinoflagellates can grow at predator: prey size ratios between 0.15:1 and 5.2:1 and exhibit optimal growth on prey approximately as large as themselves.

Within the ciliates, food collection is generally achieved in a number of ways, including suspension feeding, deposit feeding, and active predatory hunting (Capriulo, Sherr, and Sherr 1991). Compared to phagotrophic dinoflagellates, food size and geometry are generally believed to be more constrained for both loricate and aloricate ciliates in which prey size and setae length may be disproportionate with cytostome size (Heinbokel 1978; Jonsson 1986; Verity and Villareal 1986). However, there are a number of observations that naked ciliates may also ingest relatively large and bulky food particles (Gifford 1985; Smetacek 1981).

There is considerable evidence that different phytoplankton species vary in their nutritional quality for planktonic grazers (Verity and Villareal 1986). Clearly, size and shape remain first-order determinants of prey availability, and mechanical

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[1] Symposium presentation for a joint meeting of the Society of Protozoologists and the Phycological Society of America, 14–19 June 2003, Gleneden Beach, Oregon.

discrimination according to geometric criteria is one useful means of sorting among prey. Nevertheless, micrograzers are well known for their chemosensory abilities (Levandowski and Hauser 1978), which allow them to aggregate near preferred prey (Buskey and Stoecker 1989) and may even be sensitive to the physiological state of potential prey and their recent food history (Tarran 1991; Verity 1988). Moreover, there is evidence that phagotrophic flagellates and ciliates can use chemical cues to select among multiple prey, even if their food collection mechanism is best described as filter-feeders (Stoecker 1988; Tanigushi and Takeda 1988; Verity 1991a).

With respect to species-specific grazing interactions, there are a few examples showing that certain phagotrophs may be highly specialized with respect to certain food types. The marine thecate dinoflagellate *Fragilidium subglobosum,* once believed to be an obligate phototroph, was shown to be mixotrophic, apparently feeding exclusively on *Ceratium* spp. by direct engulfment (Skovgaard 1996a). Another example of food specificity is the marine dinoflagellate *Gyrodinium undulans,* which was discovered as a feeder on the planktonic diatom *Odontella aurita,* an important bloom-forming phytoplankton species in the Wadden Sea (coastal North sea) phytoplankton (Drebes and Schnepf 1998). Although *G. undulans* was also observed to feed on various eggs, it seems to be highly specialized when feeding on phytoplankton. Supplied with the food diatom *O. aurita,* the dinoflagellate could be maintained successfully in culture. However, based on many observations that were part of a phytoplankton monitoring program, Drebes and Schnepf (1998) concluded that *G. undulans* did not prey on other diatoms. Even the morphologically related *O. aurita* var *minima,* which occurred together in small numbers with the main prey species, was unaffected, and phytoplankton species other than diatoms likewise seem not to serve as food substrate for *G. undulans.*

These examples show that phagotrophic protists may be extremely selective in their choice of food, a feature generally characteristic for parasites. In fact, many heterotrophic dinoflagellates fall along a predator-parasite continuum, for which trophic classification of intermediate forms becomes somewhat arbitrary (Coats 1999). The reason for the high degree of specificity in some species is unknown. This specialization may be the ''cost'' of having evolved the ability to overcome the defense strategy of certain food species. While specificity would seem to be a poor strategy when species diversity is high, it may be quite advantageous when the preferred prey forms dense blooms.

In situ impact of microzooplankton grazing. The in situ impact of microzooplankton grazing on algal populations may be assessed by different methods (see Capriulo, Sherr, and Sherr 1991), whereby the dilution technique introduced by Landry and Hassett (Landry and Hassett 1982) is most widely used. Although the basic dilution method may be supplemented with HPLC or flow-cytometry, information with respect to species-specific aspects (both for prey and predators) of microzooplankton grazing is limited.

Another approach is to use fluorescently labeled algae to estimate microzooplankton grazing (Rublee and Gallegos 1989). This method allows the assessment of in situ microzooplankton grazing on certain species in question (Johnson, Rome, and Stoecker 2003; Stoecker, Stevens, and Gustafson 2000) by measuring the disappearance of added labeled prey over time. In addition, it also provides information about which microzooplankton species are responsible for grazing and allows calculation of species-specific clearance rates and grazing impacts (Stoecker, Stevens, and Gustafson 2000). Extended use of this technique will certainly enhance our understanding of the occurrence and importance of species-specific algae/micrograzer interactions in situ.

Numerous applications of these in-situ techniques in a variety of different marine environments have shown that micrograzers are the dominant consumers of phytoplankton production in both oligotrophic and nutrient-rich regions of ocean (Banse 1992; Capriulo, Sherr, and Sherr 1991; Sherr and Sherr 1992; Sherr and Sherr 1994). However, phytoplankton blooms do occur, indicating that there are mechanisms promoting uncoupling of phytoplankton growth and microzooplankton grazing. This scenario is best represented in coastal areas, at least seasonally, by the spring algal bloom and/or by the frequent occurrence of ''exceptional'' and often harmful summer/autumn blooms. However, there is increasing evidence that microzooplankton even play a significant role in the direct consumption of large-celled phytoplankton in highly productive coastal areas (Strom et al. 2001). Strom et al. (2001) compiled phytoplankton growth (μ) and microzooplankton grazing (g) rate data (based on dilution experiments) from coastal ecosystems over the world and showed average grazing/growth ratios ranging from 0.17 to 1.15, with an average value of g:μ taken across all experiments and studies of 0.71 (n = 177 experiments). This overall result demonstrates that microzooplankton grazing is an important—and often dominant—loss process affecting phytoplankton in coastal waters around the world.

This view is supported by data on the seasonal cycle of biomass of different protozoan groups. Hansen (1991b) showed that large (> 20 μm) naked and thecate heterotrophic dinoflagellates formed high biomass in response to the spring diatom bloom. Smetacek (1981) found that both athecate and thecate heterotrophic dinoflagellates, as well as ciliates, attained comparable biomass maxima during spring and autumn in Kiel Bight (German Baltic Sea), whereby the spring protozooplankton maximum coincided with the spring diatom bloom. Others have demonstrated dominance of thecate (Lessard 1991), athecate (Bursa 1961), or both dinoflagellate forms (Archer et al. 1996; Bralewska and Witek 1995) associated with diatom blooms in other coastal areas. This demonstrates that both naked and thecate heterotrophic dinoflagellates are able to respond numerically to diatom blooms, even when the blooms are dominated by colonial and/or spiny forms. However, high phytoplankton biomass during spring blooms as a recurrent and predictable part of succession indicates that microzooplankton populations are not able to fully control the spring diatom bloom. This might be because one of the most used arguments supporting the view of microzooplankton as important bloom controllers, i.e. microzooplankton can grow at rates comparable to their food, might not apply for the diatom spring bloom. Reviews of the phytoplankton growth literature (Smayda 1997 and references therein) note that diatom growth rates are generally quite high, whereas growth rates of the most important diatom consumers within the microzooplankton, the large heterotrophic dinoflagellates, are substantially lower (e.g. Hansen 1992; Strom and Morello 1998). Nevertheless, microzooplankton grazing might partly be responsible for some of the large annual variations in spring phytoplankton biomass maxima. Furthermore, in view of selective feeding, microzooplankton might alter phytoplankton species succession patterns. For example, *Gyrodinium undulans* exclusively feeds on *Odontella aurita* (Drebes and Schnepf 1998) leaving behind dead cells that are easy to recognize by clumped discolored chloroplasts and a thin snorkel-like feeding tube. The percentage of *O. aurita* cells affected by this dinoflagellate varied considerably in different years, sometimes reaching epidemic dimensions with 85% of the *O. aurita* population damaged by *G. undulans* (Drebes and Schnepf 1998).

Table **1**. Compilation of peak abundances of different protozooplankton species.

Species	Cells ml^{-1}	Locality	Ref.[a]
Ciliates			
Rimostrombidium caudatum	898	Brackish inland pond, northern Germany	2
Strombidium reticulatum	1242	Flodevigen Bay, southern Norway	5
Tintinnopsis beroidea	729	Flodevigen Bay, southern Norway	5
Tiarina fusus	34000	southern Norway	6
Tintinnids (mainly *Helicostomella subulata*)	118	coastal North Sea	1
Strombidium oculatum	300	rock pool	7
undet. gymnostome ciliate	600	Alaska	8
Lohmaniella oviformis	125	Limfjord, Denmark	3
Helicostomella subulata	40	Limfjord, Denmark	3
Strombidium lingulum	1500	Fjord, British Columbia	10
Strombidium cf. *capitatum*	53	Bay of Villefranche	14
Helicostomella subulata	100	Bedford Basis, Nova Scotia	13
Dinoflagellates			
Oblea rotunda	2500	Brackish inland water pond, northern Germany	15
Protoperidinium divergens	17	Oslo Fjord	12
Oxyrrhis marina	209	Kunsan Port, Korea	9
Polykrikos kofoidii	20	Norwegian coast	17
Gyrodinium spirale	110	Norwegian coast	17
Gyrodinium dominans	100	Seto Inland Sea	11
Polykrikos schwarzii	38	Argentine Sea	4
Polykrikos kofoidii	28	Lisbon coast	16

[a] (1) Admiraal and Venekamp 1986; (2) Agatha and Riedel-Lorjé 1998; (3) Andersen and Sörensen 1986; (4) Carreto et al. 1986; (5) Dale and Dahl 1987a; (6) Dale and Dahl 1987b; (7) Fauré-Fremiet 1948; (8) Holm-Hansen, Taylor, and Barsdate 1970; (9) Jeong et al. 2003b; (10) Montagnes and Humphrey 1998; (11) Nakamura, Suzuki, and Hiromi 1995a; (12) Paasche and Kristiansen 1982; (13) Paranjape 1980; (14) Rassoulzadegan 1977; (15) Riedel-Lorjé et al. 1997; (16) Sampayo 1998; (17) Tangen 1980.

Field evidence for bloom control. There are some limited field data indicating that high zooplankton grazing pressure may be causatively linked to the prevention of algal blooms (Watras et al. 1985). Work like that of Watras et al., who combined data from a multi-year time-series with determinations of species-specific grazing rates, is very rare. Because research activity is typically enhanced during red-tide events, there are several additional reports of high numbers of micrograzers during and after blooms, indicating that microzooplankton grazing substantially contribute to the decline of high microalgal biomass (Admiraal and Venekamp 1986; Carreto et al. 1986; Holmes, Williams, and Eppley 1967; Matsuyama, Miyamoto, and Kotani 1999; Nakamura, Suzuki, and Hiromi 1995b; Nakamura, Suzuki, and Hiromi 1996; Needler 1949; Prakash 1963; Sampayo 1998). For example, Admiraal and Venekamp (1986) found extremely dense populations of two tintinnid species in North Sea coastal waters to actively graze single cells of the colony-forming alga, *Phaeocystis pouchetii*, during the spring bloom. At the end of the bloom, biomass of tintinnids equaled or even exceeded that of *Phaeocystis*, indicating that microzooplankton grazing prevented further growth of the *Phaeocystis* spring bloom (Admiraal and Venekamp 1986). Likewise, field investigations of Weisse and Scheffel-Möser (1990) showed that high microzooplankton grazing rates substantially reduced the accumulation of *Phaeocystis* sp. during bloom development. Furthermore, grazing rates increased over the course of the bloom and eventually exceeded *Phaeocystis* growth rates, indicating that microzooplankton substantially contributed to the decline in the *Phaeocystis* bloom. Heterotrophic dinoflagellates, as well as tintinnids, have been reported to have completely consumed *Gyrodinium mikimotoi* red-tides within a few days (Nakamura, Suzuki, and Hiromi 1995b; Nakamura, Suzuki, and Hiromi 1996). It is important to note that in most cases only a single protozoan species was involved in the decline of the algal species in question, underlining the importance of species interactions for bloom control.

In contrast to the examples described above, there are a number of papers describing a remarkable impoverishment of micrograzers in certain algal blooms. For example, Bjornsen and Nielsen (1991) found a drastic reduction in microzooplankton concentration in the Kattegat at a depth coinciding with a subsurface layer of *Gyrodinium aureolum*. Likewise, during the huge 1988 bloom of *Chrysochromulina polylepis* in the North Sea, Nielsen, Kiorboe, and Bjornsen (1990) observed that no potential predators on *C. polylepis* were present in the pycnocline, where the highest concentration of algae were recorded.

Several papers report extremely high maximum abundances of single microzooplankton species in nature (summarized in Table 1). These high abundances probably can not be fully explained by protozooplankton growth alone, and may be at least partly due to physical processes. These data nevertheless clearly show that microzooplankton species readily transform high phytoplankton biomass (blooms) to high microzooplankton biomass and thus are able to control and remove algal blooms. These observations of single species protozoan ''blooms'' again underscore the importance of species-specific aspects of algal/protozoan interactions. Apart from these observations of microzooplankton abundance peaks, there are only a few reports on the formation and decline of blooms of microzooplankton species in situ. The scarcity of such data may be due to the rarity of such ''blooms'', or may equally result from their transient nature, both in time and space. Recurrent blooms of the large heterotrophic dinoflagellate *Noctiluca scintillans*, one of the most common ''red tide'' organisms, are remarkable exceptions. *N. scintillans* is a voracious feeder, ingesting all particles which it can engulf, that is likely able to exert significant feeding pressure on phytoplankton (Elbrächter and Qi 1998 and references therein).

Whereas ''bloom'' formation of protistan species certainly reflects prior existence of optimal food conditions, the build-up of high micrograzer abundance is also most probably restricted to periods when top-down control on microzooplankton is released.

Top-down control of microzooplankton. Smetacek's (1981) detailed analysis of Kiel Bayś annual cycle confirmed that the size of the micrograzer population is apparently controlled more through predation by mesozooplankton than by the quantity and quality of the food supply. Micrograzers are now recognized as an important link to larger metazoans like juvenile (Merrel and Stoecker 1998) and adult copepods (Stoecker and McDowell Capuzzo 1990), larval and post-larval ctenophores (Stoecker et al. 1987), crab larvae (Sulkin et al. 1998), and fish larvae (Fukami et al. 1999). In addition to being grazed by mesozooplankton, micrograzer communities appear to contain quite a large numbers of trophic links. Several mixotrophic dinoflagellates have been described to ingest ciliates (Biecheler 1952; Bockstahler and Coats 1993a, b; Jacobson and Anderson 1996; Li et al. 1996). For instance, *Ceratium furca* preys mainly on choreotrich ciliates of the genus *Strobilidium* (Smalley, Coats, and Adams 1999), and the impact of *C. furca* feeding on ciliate prey populations may be quite high, i.e. averaging 67% of *Strobilidium* spp. removed d^{-1} (Smalley and Coats 2002). The mixotrophic dinoflagellate *Gyrodinium instriatum* has been reported to prey on a number of loricated ciliates, some of them several times larger in volume than the dinoflagellate itself (Uchida, Kamiyama, and Matsuyama 1997). Heterotrophic species of the dinoflagellate genus *Dinophysis* feed by means of a peduncle on the ciliate *Tiarina fusus*, which itself feeds on autotrophic species of *Dinophysis* by engulfing them (Hansen 1991a). Thus, a predatory ciliate may become the prey of the dinoflagellate it tried to consume.

Given this wide range of potential predators of microzooplankton, multi-trophic level interactions between algae, micrograzers, and their predators are likely to occur. It has been proposed that omnivorous copepods can contribute to blooms of toxic phytoplankters by consuming heterotrophic protists that might otherwise have prevented bloom formation trough grazing activity (Caron et al. 1989; Hansen et al. 1993; Hansen and van Boekel 1991). For example, laboratory experiments of Hansen et al. (1993) showed that mesozooplankton predation on herbivorous ciliates and heterotrophic dinoflagellates that consume single cells of *Phaeocystis* can considerably reduce the overall grazing pressure and thus may enhance the formation of *Phaeocystis* blooms.

However, micrograzers apparently have evolved some strategies for use as defense mechanisms against their predators, including extrusomes (Harumoto 1994; Miyake and Harumoto 1996) and bioluminescence (Abrahams and Townsend 1993). Although almost nothing is known about morphological changes of marine micrograzers in response to their grazers, such responses are well known from freshwater species (see Strom 2002 and references therein). Finally, swimming behavior of ciliates has been described as a potent mediator of escape from copepods (Broglio, Johansson, and Jonsson 2001; Jakobsen 2001, 2002).

Laboratory findings. Many studies have analyzed various aspects of growth and feeding of micrograzer species in culture (Table 2), with many especially designed to study the interactions of micrograzers with bloom-forming and/or toxic algae species. However, there are a number of confusing reports with different results for grazing studies on harmful algal species, some showing no effect on grazers, while others show various adverse effects. These inconsistent results may indicate that there is a great range in responses of various protozoan species to a given algal species. However, in many cases, the chemical identity of deterrents or lethal toxins that influence interactions with protozoan grazers are unknown, and hence the ''toxicity'' of the algal culture has not been verified or measured in a standardized and comparable way. In the case of ''known'' algal biotoxins, it has been repeatedly established that cultured strains of toxic algae are typically less toxic than those collected from natural populations (Cembella, Therriault, and Béland 1988; Edvardsen 1993; White 1986). Cultured strains may also vary considerably with respect to cellular toxin content (Anderson 1990; Chang et al. 1997; Edvardsen and Paasche 1998; Parkhill and Cembella 1999) and toxin profile (Cembella 1998). Furthermore, toxin production may be affected by a variety of environmental factors such as nutrient status of the algae (e.g. Johansson and Granéli 1999). In the case of extracellular toxins, chemical/biological factors affecting toxin exudation and inactivation/degradation may largely control toxicity, but are not well understood. When *Prymnesium parvum*, for example, was grown under conditions that appeared not to elicit toxic effects, it was rapidly ingested by and sustained growth of *O. marina*, whereas *O. marina* was rapidly killed by lytic extracellular toxins when offered highly toxic *Prymnesium parvum* as prey (Tillmann 2003).

As long as the chemical identity of allelochemicals involved in algae/micrograzer interactions remains unknown, and hence the chemical detection and quantification of the substances impossible, it will be difficult to compare laboratory results, or to relate laboratory findings to field situations.

Phytoplankton defense strategies. The importance of grazing losses as a major source of phytoplankton mortality suggests an intense selective pressure for the evolution of defenses against grazers (Smetacek 2001; Strom 2002; Verity and Smetacek 1996). The range of defense systems in plankton is only now coming to light. Plankton cells can escape by swimming or by mechanical protection; mineral and tough organic cell walls ward off piercers or crushers. In adapting to deter predators, phytoplankton species have increased in size, formed large chains and colonies, or grown spines. Last, but not least, there are noxious chemicals which also provide defense (Smetacek 2001). If a certain algal species is difficult to graze, e.g. due to size or species-specific defense mechanisms, the reduced grazing pressure will certainly favor bloom development.

Morphological defense. At the predator's species level, size and shape remain first-order determinants of prey suitability. The formation of colonies and chains, which simply increases size, may thus act as an anti-grazer feature. In addition, horns, spines, and other protuberances, as well as mucilages, are generally believed to inhibit or discourage grazers. For example, Verity and Villareal (1986) found that two species of coastal tintinnids grew poorly on diatoms possessing siliceous setae or chitinous threads. The same tintinnid species grew rapidly on the same diatom species when the chitinous threads were reduced by culturing the algae on a shaker table. However, there is obviously no single defense system that functions perfectly against the whole range of potential predators. With respect to size, spines, or chain formation, there are several examples of how individual micrograzers may be able to overcome these constraints. Pallium feeding heterotrophic dinoflagellates are known to feed on food particles larger then themselves, including long diatom chains (Jacobson and Anderson 1986). *Polykrikos kofoidii* has been observed to attach to chains of *Gymnodinium catenatum* and break them (Sampayo 1998), thus being able to ingest smaller parts of the chains. Likewise, the naked dinoflagellate *Gyrodinium spirale* is apparently able to break some diatom chains (e.g. *Skeletonema*), transforming the prey into a round food package and then ingesting the whole

Table **2**. Literature compilation on protozooplankton species successfully cultured (Nano = Nanoflagellates, Raphido = Raphidophytes, Dino = Dinoflagellates, Dia = Diatoms).

Microzooplankton species	Prey type	Reference[a]
Ciliates		
Amphorella quadrilineata	Nano	18
Balanion comatum	Nano	20, 46
Balanion sp.	Dino	53
Coxliella sp.	Nano	60
Diophrys sp.	Nano	33
Eutintinnus pectinis	Nano	18
Fabrea salina	Nano	48
Favella azoica	Dino	30
Favella ehrenbergii	Raphido, Dino, Nano	55, 31, 11, 13, 15, 7, 46
Favella sp.	Raphido, Dino, Nano	6, 1, 69, 5, 25, 53, 54
Favella taraikaensis	Raphido, Dino, Nano	62, 31, 30
Helicostomella subulata	Nano	45, 18
Laboea strobila	Nano	56
Lohmaniella oviformis	Nano	61
Lohmaniella sp.	Nano	8
Lohmaniella spiralis	Nano	29, 47
Rimostrombidium caudatum	Nano	46
Rimostrombidium conicum	Nano	61
Rimostrombidium veniliae	Dino	46
Strobilidium neptuni	Nano	36
Strobilidium spiralis	Nano	56
Strobilidium veniliae	Nano	36
Strombidinopsis cheshiri	Dia	37
Strombidinopsis multiauris	Dino	38
Strombidinopsis acuminatum	Nano, Dino	59, 14
Strombidinopsis sp.	Dino	27
Strombidium capitatum	Nano	36, 56
Strombidium conicum	Nano	56
Strombidium reticulatum	Nano	29
Strombidium siculum	Nano	36
Strombidium sulcatum	Nano	2, 9
Strombidium vestitium	Nano	61
Tiarina fusus	Raphido, Dino	28, 33
Tintinnopsis tubulosoides	Raphido	69
Tintinnopsis cf. *beroidea*	Nano	18
Tintinnopsis cf. *acuminata*	Nano	18
Tintinnopsis acuminata	Nano	67
Tintinnopsis dadayi	Nano	68
Tintinnopsis vasculum	Nano	67
Uronema sp.	Nano	59
Dinoflagellates		
Amphidinium crassum	Nano	12
Amphidinium longum	Nano	60
Amphidinium sp.	Nano	59
Diplopsalis lenticula	Dino, Dia	42
Fragilidium cf. *mexicanum*	Dino	26
Fragilidium subglobosum	Dino	49–51
Gymnodinium fungiforme	Nano	52
Gymnodinium sp.	Nano	20
Gymnodinium sp.	Nano	57
Gyrodinium dominans	Raphido, Dino, Dia, Nano	12, 44, 41, 40, 61, 46
Gyrodinium fusiforme	Dino, Dia	44
Gyrodinium spirale	Dino, Dia	12
Katodinium glaucum	Dino	44
Noctiluca scintillans	Raphido, Dino, Nano	32, 25, 39, 59
Oblea rotunda	Raphido, Dino, Dia, Nana	58, 65
Oxyrrhis marina	Raphido, Dino, Nano, Dia	60, 63, 10, 22, 16, 65, 64, 17, 46
Polykrikos kofoidii	Dino	34, 35, 21, 24
Protoperidinium cf. *divergens*	Dino	23
Protoperidinium crassipes	Dino	23
Protoperidinium hirobis	Dia	19
Protoperidinium huberi	Dia, Dino	4
Protoperidinium pallidum	Dia, Dino, Nano	43
Protoperidinium pellucidum	Dia, Dino	12, 3
Protoperidinium steinii	Dia, Dino, Nano	43
Zygabicodinium lenticulatum	Dia, Dino, Nano	43

Table **2**. Continued

Microzooplankton species	Prey type	Reference[a]
Heliozoan		
Heterophrys marina	Nano, Dino	66

[a] (1) Aelion and Chisholm 1985; (2) Bernard and Rassoulzadegan 1990; (3) Buskey 1997; (4) Buskey, Coulter, and Brown 1994; (5) Buskey and Stoecker 1988; (6) Buskey and Stoecker 1989; (7) Carlsson, Granéli, and Olsson 1990; (8) Chen and Chang 1999; (9) Dolan and Simek 1997; (10) Goldman, Dennett, and Gordin 1989; (11) Hansen 1989; (12) Hansen 1992; (13) Hansen 1995b; (14) Hansen 1995a; (15) Hansen, Cembella, and Moestrup 1992; (16) Hansen et al. 1993; (17) Hansen, Witte, and Passarge 1996; (18) Heinbokel 1978; (19) Jacobson and Anderson 1993; (20) Jakobsen and Hansen 1997; (21) Jeong et al. 2001a; (22) Jeong et al. 2001b; (23) Jeong and Latz 1994; (24) Jeong et al. 2003a; (25) Jeong and Shim 1996; (26) Jeong et al. 1999b; (27) Jeong et al. 1999a; (28) Jeong et al. 2002a; (29) Jonsson 1986; (30) Kamiyama 1997; (31) Kamiyama and Arima 2001; (32) Kiorboe and Titelman 1998; (33) Klekowski and Tumantseva 1981; (34) Matsuoka, Cho, and Jacobson 2000; (35) Matsuyama, Miyamoto, and Kotani 1999; (36) Montagnes 1996; (37) Montagnes, Berger, and Taylor 1996; (38) Montagnes and Lessard 1999; (39) Nakamura 1998; (40) Nakamura, Suzuki, and Hiromi 1995a; (41) Nakamura, Yamazaki, and Hiromi 1992; (42) Naustvoll 1998; (43) Naustvoll 2000a; (44) Naustvoll 2000b; (45) Paranjape 1980; (46) Pedersen and Hansen (2003); (47) Rassoulzadegan 1982; (48) Repak 1983; (49) Skovgaard 1996a; (50) Skovgaard 1996b; (51) Skovgaard, Hansen, and Stoecker 2000; (52) Spero and Morée 1981; (53) Stoecker and Evans 1985; (54) Stoecker and Guillard 1982; (55) Stoecker, Guillard, and Kavee 1981; (56) Stoecker and Michaels 1991; (57) Strom 1991; (58) Strom and Buskey 1993; (59) Strom and Morello 1998; (60) Strom et al. 2003b; (61) Tang, Jakobsen, and Visser 2001; (62) Taniguchi and Kawakami 1985; (63) Tarran 1991; (64) Tillmann 2003; (65) Tillmann and Reckermann 2002; (66) Tobiesen 1991; (67) Verity 1985; (68) Verity 1991b; (69) Verity and Stoecker 1982.

colony (Hansen and Calado 1999). Another example of dinoflagellates ''reshaping'' prey, that due to size and large spines would otherwise seem too bulky, is the mixotrophic dinoflagellate *Fragilidium subglobosum*, which ingests *Ceratium* species much larger than itself. Here, the thecal plates and horns of *Ceratium* are gradually dissolved during the ingestion process (Skovgaard 1996a).

The role of extrusomes, common to most ciliates, dinoflagellates, raphidophytes and some other taxa, has long been a puzzle. For microzooplankton species, recent results suggest that trichocysts of *Polykrikos* are used to capture prey (Matsuoka, Cho, and Jacobson 2000), and, for ciliates, trichocysts may function as defense organelles against many predatory ciliates (Harumoto 1994; Miyake and Harumoto 1996). A comparable defense strategy was recently described by Tillmann and Reckermann (2002) for the algal species *Fibrocapsa japonica* which extrudes trichocysts when contacted by the pallium of *Oblea rotunda*. This prevents further development of the pallium, eventually allowing *F. japonica* to escape. Likewise, Ukeles and Sweeney (1969) provided at least some indirect evidence that trichocysts of autotrophic dinoflagellates can inhibit feeding of marine invertebrates to some extent.

Behavioral defense. Behavioral aspects of phytoplankton that may affect micrograzer feeding interactions have received little attention. With the exception of diatoms and cyanobacteria, most phytoplankton species are motile. Algal motility has been generally implicated with directional movement toward light or enhanced nutrient concentration, but its role in grazer interactions has rarely been studied. Studies of the heterotrophic dinoflagellates *Protoperidinium pellucidum* (Buskey 1997), *Oblea rotunda* (Strom and Buskey 1993), and *Noctiluca scintillans* (Kiorboe and Titelman 1998) have shown lower capture success, grazing rate, and growth rate on motile dinoflagellates relative to non-motile diatom prey. The latter authors noted that *Heterocapsa triquetra* frequently tumbled and continued to swim after contacting a mucus thread of *Noctiluca scintillans*, thus avoiding entanglement and capture (Kiorboe and Titelman 1998). In quantifying behavioral aspects of *Oblea rotunda* feeding on the raphidophyte *Fibrocapsa japonica*, Tillmann and Reckermann (2002) showed that algal motility can be a very effective defense mechanism against pallium-feeding dinoflagellates. Because *F. japonica* has the ability to escape predation by continued swimming, only about 8% of encounters characterized by the predatorś typical ''pre-feeding'' behavior led to successful capture and digestion.

In addition to being a direct escape mechanism, algal motility allows for the formation of dense patches, both horizontally and vertically. However, the advantages gained by motile organisms aggregating in patches or dense layers are poorly understood. One strategy is that of layer formation at the particular depth where nutrient availability and irradiance is balanced for growth, even if that growth rate is low for the species in question (Cullen and MacIntyre 1998). In addition, aggregation may help avoid dispersal of an algal population by flushing (Anderson and Stolzenbach 1985), locally increase the mating success of gametes (Wyatt and Jenkinson 1997), or reduce turbulence (Berdalet and Estrada 1993).

Whatever the reasons that lead to the formation of dense layers or patches, this behavior may also impose locally unfavorable conditions like nutrient limitation or high pH. Most important, however, patch formation may enhance the risk of being grazed, as micrograzers are known to actively exploit and remain within patches of food (Buskey and Stoecker 1988). Consequently, the exudation of noxious chemicals seems to be a good strategy to prevent micrograzers from invading dense algal layers. Indeed, a number of algal species (*Alexandrium* spp., *Gyrodinium aureolum*, *Chrysochromulina polylepis*), which often appear in dense layers associated with the pycnocline (Richardson 1997 and references therein), are known to produce extracellular toxins (Gentien 1998; Schmidt and Hansen 2001; Tillmann and John 2002). Hence, patch formation may allow concentrations of extracellular chemicals to reach levels high enough to act efficiently against micrograzers and thus may confer an enhanced defense capability (Vardi et al. 2002). In this special case, the proposed defense system combines motility, behavior, and toxin production.

Chemical defense. The chemical defense ecology of marine unicellular plankton was recently reviewed by Wolfe (2000). Compared to terrestrial ecology, chemical signals that determine interactions between marine micrograzers and prey are poorly known, although they are believed to contribute to food selection, avoidance, and defense, thus having the potential to affect trophic structure and large-scale features such as algal blooms.

Chemical defense might be expressed as acute mortality of micrograzers or by sublethal effects like reduced feeding rates or reduced grazer productivity. From an ecological perspective, whether a predator avoids toxic algae or is killed by the algal toxin has importantly different consequences. In the first case, the predator is able to continue feeding on other co-existing

Table **3**. Compilation of laboratory findings where algal species caused feeding inhibition (FI) or acute toxicity (AT) towards certain micrograzer species.

Phytoplankton species	Micrograzer species	Effect	Reference[a]
Chrysochromulina polylepis	*Oxyrrhis marina*	FI	7
	Favella ehrenbergii,		1
	Heterophrys marina		16
Prymnesium parvum	*Oxyrrhis marina*	FI, **AT**	14
	Euplotes affinis		6
Alexandrium spp.	*Oblea rotunda*	**AT**	15
	Oxyrrhis marina		15
	Favella ehrenbergii		5, 3
	Polykrikos kofoidii		11
	Amphidinium crassum		Tillmann unpubl.
	Rimostrombidium caudatum		Tillmann unpubl.
Heterosigma akashiwo (=*Olistodiscus luteus*)	*Tintinnopsis tubulosoides*	FI, **AT**	17
	Favella sp.		17
	Synchaeta cecilia		2
Emiliania huxleyi	*Coxliella* sp.	FI	13
	Strombidinopsis sp.		
	Metacylis sp.		
	Amphidinium longum		
	Gymnodinium sp.		
Heterocapsa circularisquama	*Favella taraikaensis*	FI, **AT**	9, 8, 10
	Brachionus plicatilis		12
Gyrodinium aureolum (=*Karenia mikimotoi*)	*Favella ehrenbergii*	FI, **AT**	4

[a] (1) Carlsson, Granéli, and Olsson 1990; (2) Egloff 1986; (3) Hansen 1989; (4) Hansen 1995b; (5) Hansen, Cembella, and Moestrup 1992; (6) Johansson 2000; (7) John, Tillmann, and Medlin 2002; (8) Kamiyama 1997; (9) Kamiyama and Arima 1997; (10) Kamiyama and Arima 2001; (11) Matsuoka, Cho, and Jacobson 2000; (12) Sato, et al. 2002; (13) Strom et al. 2003b; (14) Tillmann 2003; (15) Tillmann and John 2002; (16) Tobiesen 1991; (17) Verity and Stoecker 1982.

phytoplankton species, thereby releasing the toxic species from competition. In addition, as many HAB species are known to be mixotrophic, zooplankton grazing on other algae and subsequent DOC release (Strom et al. 1997) might stimulate the growth of bacteria, which in turn might benefit the mixotrophic HAB species (Jones, Leadbeater, and Green 1993; Nygaard and Tobiesen 1993). By contrast, elimination of grazers also relieves grazing pressure on competing algal species, making it more difficult to explain the formation of monospecific blooms. Nevertheless, there are several phytoplankton species for which lethal effects on micrograzers have been reported (Table 3). In most cases, the lethal effects could be attributed to the presence of extracellular toxins found in the culture medium (Hansen 1989; Tillmann and John 2002; Tillmann 2003), but for some species direct contact with the toxic algal cells may be involved (Uchida et al. 1995; Kamiyama and Arima 1997). There is no clear evidence that ingestion and hence incorporation of intracellular algal toxins is related to negative effects on micrograzers. Grazing experiments using mixed diets, however, have demonstrated that the tintinnid *Favella ehrenbergii* cannot selectively avoid ingestion of *Gyrodinium aureolum*, with feeding on this toxic algae resulting in suppressed growth of the ciliate (Hansen 1995b). Mortality of *F. ehrenbergii* upon addition of dense *G. aureolum* cultures approached, but never surpassed that due to pure starvation, making it unlikely that incorporated toxins exerted lethal effects. In the case of *Alexandrium*, it was recently speculated that ingestion of PSP-toxic *A. tamarense* cells was the cause of *P. kofoidii* cell lysis (Cho and Matsuoka 2000). However, results presented by Tillmann and John (2002) clearly showed that lytic toxins of *Alexandrium* spp., being distinct from PSP, are extracellular, making it unlikely that cell lysis of *P. kofoidii* was causatively linked to ingestion.

The power to immobilize or kill potential predators surely is of adaptive significance for a HAB species in the formation of dense and long-lasting blooms. However, it does not necessarily follow that such lytic compounds evolved in response to predation, because it is likely that the same compounds also affect interactions within the trophic level (i.e. allelophathic algae/algae interaction). For mixotrophic algae, it may even be speculated that toxins serve to immobilize and kill potential prey organisms (Skovgaard and Hansen 2003; Tillmann 1998). For example, it was recently shown that the micrograzer *Oxyrrhis marina* is not only rapidly killed by toxins of *Prymnesium parvum*, but is subsequently ingested by the mixotrophic algae. In this case, the normal direction of grazing interactions between protozoa and algae is completely reversed (Tillmann 2003).

Defense mechanisms that have lethal effects are relatively well studied because they are easy to detect and quantify, but considerably less is known about sublethal chemical defense. In a comparative approach using toxic and non-toxic clones of *Chrysochromulina polylepis* as prey, John, Tillmann, and Medlin (2002) confirmed profound differences in ingestion, clearance, division, and gross growth efficiency of *O. marina*. Even at algal concentrations of 400×10^3 ml^{-1}, *O. marina* was not killed by the presence or ingestion of toxic *C. polylepis*, indicating that these toxins deter grazers. Perhaps the best studied sublethal chemical defense system of marine protists is the production and breakdown of dimethylsulfoniopropionate (DMSP) by numerous phytoplankton species (Wolfe and Steinke 1996; Wolfe, Steinke, and Kirst 1997; Strom et al. 2003a, b). In laboratory experiments, five out of six tested protistan grazer species showed lower feeding rates on strains of *Emiliania huxleyi* that had high DMSP lyase activity. Reduced feeding was consistent with lower population growth rates of grazers (Strom et al. 2003b). In a companion paper, Strom et al. (2003a) presented evidence that addition of pure DMSP, but not its cleavage products DMS or acrylate, was responsible for reduced protistan grazing rates. Hence, this is one rare example where the chemical substances involved in an algae-micrograzer defense mechanism have been identified.

There has been recent confirmation that a number of diatom species negatively influence the reproduction of herbivorous co-

pepods (Ban et al. 1997 and references therein), and this effect has been attributed to the presence of reactive aldehydes acting as mitotic inhibitors (Miralto et al. 1999; Pohnert et al. 2002). Diatoms reduce the risk of self-poisoning by the aggressive mitotic inhibitors because formation of the aldehydes is enzymatically initiated immediately after cell damage (Pohnert 2002). While effects of these compounds on copepod reproduction are quite well studied, virtually nothing is known about their potential activity as a defense system against protistan grazers.

Micrograzers as bloom control strategy. Compared to the widespread and often effective use of biological control in terrestrial ecosystems, attempts to apply biological control agents against algal blooms are in their infancy. Identified potential control agents include parasites (Coats et al. 1996), bacteria (Yoshinaga et al. 1998), viruses (Tarutani, Nagasaki, and Yamaguchi 2000), allelopathic algae/substances (Legrand et al. 2003), and micrograzers (Jeong 2001; Jeong et al. 2003b). The use of organisms as degradable and natural organic compounds could be an advantage compared to chemical [e.g. copper sulfate, (Carmichael 1994), NaOCl, (Jeong et al. 2002b)] or mechanical [e.g. clay flocculation, (Sengco et al. 2001)] control measures. However, attempts to realize the idea to use certain micrograzers to control red tides are very rare.

The idea to introduce mass cultured micrograzers to control algal bloom is supported by two main potential merits: 1) heterotrophic micrograzers are known to be good food for a large number of metazooplankton species and therefore are likely to be at least partly transferred to higher trophic levels after ''their job is done;'' 2) introduced micrograzers would be expected to grow and rapidly increase their numbers and may therefore be able to dissipate large-scale blooms even when a small initial addition of the grazers.

However, several potential drawbacks must be kept in mind. First, introduction of micrograzers at an early stage of bloom development of a HAB species might cause preferential grazing on co-occurring ''good'' algae, thereby releasing HAB species from competition. This might even stimulate HAB formation. Second, although many protists are known to be optimal food for higher trophic grazers, there is a risk that high densities of micrograzers might cause an imbalance in the food web. Third, while it is well known that copepods can accumulate and transfer phytoplankton toxins through the food web, sometimes with lethal effects on zooplanktivorous fish (White 1981; Turriff, Runge, and Cembella 1995; Tester, Turner, and Shea et al. 2000), little is known about the ability of micrograzers to accumulate algal biotoxins. By grazing certain HAB species not eaten by larger zooplankton, micrograzers may even enhance vectorisation of toxins to higher trophic levels. There are some limited and mainly indirect indications that micrograzers are involved in toxin denaturation. Sampayo (1998) described a bloom of *Gymnodinium catenatum* that declined rapidly due to heavy grazing of a large population of *Polykrikos kofoidii*. Toxin concentrations in bivalves of the area declined rapidly after the bloom breakdown, indicating that feeding and population growth of *P. kofoidii* may have speeded up toxin depuration in the bivalves. During blooms of *Dinophysis acuminata*, the tintinnid *Favella serrata* was observed to feed on the toxin dinoflagellates (Maneiro et al. 2000). Ocaidic acid (OA) content found in different seston fractions showed a good correlation with *F. serrata*, indicating that tintinnids can transfer OA to higher trophic levels.

However, there is a clear need for detailed laboratory studies analyzing toxin transfer and retention in systems consisting of harmful algae, micrograzers, and copepods. This issue was recently addressed in two papers by Jeong et al. (2001b, 2003a). The micrograzer *Oxyrrhis marina* was shown to be a potential trophic link between toxic dinoflagellates and copepods that did not feed directly on the algae (Jeong et al. 2001b). However, while the copepod *Acartia* spp. ingested *O. marina* at high rates when *O. marina* was fed the non-toxic control species *Prorocentrum*, ingestion of Oxyrrhis satiated with toxic *Amphidinium* was almost zero. High ingestion rates of *Acartia* on *Oxyrrhis* could be restored after starving *Amphidinium* satiated *Oxyrrhis* for a few days, indicating that these micrograzers may have an ability to detoxify and/or excrete the phytoplankton toxins. Unfortunately, toxicity was measured for *Amphidinium carterae* only, not for *O. marina*, and thus quantitative statements about toxin accumulation, retention, or detoxification are impossible. This issue was recently addressed in more detail in a second paper of Jeong et al. (2003a), who conducted laboratory experiments to study retention and dissipation of PSP toxins by the heterotrophic dinoflagellate *Polykrikos kofoidii* fed with *Gymnodinium catenatum*. They reported a retention value (ratio of the toxicity retained in the body of a grazer to the total toxicity of the prey ingested) for *P. kofoidii* feeding on *G. catenatum* of 66%, much higher compared to retention values of copepods feeding on *Alexandrium* spp. ($<$ 10%, Teegarden and Cembella 1996). As in *O. marina* fed *A. carterae*, PSP toxins in *P. kofoidii* exponentially decreased upon starvation with a decay constant of 0.059 h^{-1} (Jeong et al. 2003a). In this case, however, it is not known whether *P. kofoidii* with high amounts of accumulated PSP toxins will or will not be subject to copepod grazing (as might be deduced from Jeong's findings presented above). Clearly more studies are needed on this topic to confirm whether micrograzing will be a link (vectorisation of toxins to higher trophic levels) or a sink for algal toxins.

Improved culture techniques have allowed a large number of microzooplankton species to be brought into culture and used in laboratory experiments (compiled in Table 2), although their number still appears to be small compared to the total number of microzooplankton species present in the ocean. However, there is likely a significant difference between culturing a given micrograzer species on laboratory scale for few weeks and the establishment of mass cultures reliably available at times they are needed for controlling blooms (i.e. when blooms appear).

One problem with respect to maintaining mass cultures of micrograzers might be clonal aging. For ciliates, isolated clones typically maintain a constant growth rate for $>$ 100 generations, and by $\sim$ 200 generations after conjugation, most clones are extinct (Bell 1988). Clonal aging and self conjugation were recently identified as factors causing high sub-clonal variability in ciliate growth rate, with high mutational load assumed to cause abnormally low growth rates in culture (Montagnes, Berger, and Taylor 1996). However, almost nothing is known with respect to clonal aging in non-ciliate micrograzer species.

Very recently, the development of an automatic system for mass culturing *O. marina* has been described (Jeong et al. 2003b). The authors explored the potential use of *O. marina* in controlling algal blooms by not only performing laboratory experiments, but also conducting mesocosm experiments using cultured and natural populations of *Heterosigma akashiwo*. In these mesocosms, cultured *O. marina* grew well and reduced natural bloom populations of *H. akashiwo* within a few days (Jeong et al. 2003b). This approach is currently being expanded by introducing mass cultured *Oxyrrhis* into red tide waters containing *Heterosigma akashiwo* in a semi-enclosed small bay in Korea (Hae Jin Jeong, pers. commun.).

Oxyrrhis marina has a number of advantages with respect to mass-culturing and application as biological control: 1) *O. marina* is extremely easy to grow (in fact, it is common knowledge among scientist working with protistan cultures that it is more

difficult to remove *O. marina* than to bring it into culture); 2) *O. marina* can grow quite fast (μmax up to 1.43 d^{-1}, Jeong et al. 2003b); 3) *O. marina* has been shown to be able to feed on a large number of different algal species, including a number of HABs (see Table 2); 4) *O. marina* is known to be excellent prey for a number of copepods (Klein Breteler 1980; Klein Breteler et al. 1999).

Among the bloom-forming and/or potentially toxic algae tested in growth experiments, *O. marina* has been shown to feed and grow on a number of species including *Fibrocapsa japonica* (Tillmann and Reckermann 2002), *Amphidinium carterae* (Jeong et al. 2001b), and *Heterosigma akashiwo* (Jeong et al. 2003b). On the other hand, *O. marina* is negatively affected by other algal species. *O. marina* exhibited strongly reduced grazing rates on a toxic clone of *Chrysochromulina polylepis* (John, Tillmann, and Medlin 2002) and is obviously sensitive to lytic extracellular toxins produced by *Prymnesium parvum* (Tillmann 2003) and *Alexandrium* spp. (Tillmann and John 2002), with the strength of negative effects varying considerably among different species, different strains of the same species, and different culture conditions. As discussed earlier, detection and quantification of allelochemicals involved in algae/micrograzer interactions is impossible due to unknown chemical identity to the substances. The lack of chemical identity also makes it difficult to rule out the possibility that a grazer species found to feed on a given algal strain with impunity, may fail to control the alga under different conditions (environmental condition, different strains, etc.).

To conclude, before mass-cultured protistan grazers can be successfully applied in the field, more basic research is needed to understand the biological and environmental regulation of species-specific interactions between microalgal species and protistan grazers.

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Received 08/20/03; accepted 08/20/03