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Capacity of herbivorous protists to control initiation and development of mass phytoplankton blooms

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ABSTRACT: Microzooplankton, heterotrophic organisms 20 to 200 µm in size and mainly phagotrophic protists, are recognized as the dominant consumers of phytoplankton in all regions of the sea. During his long career, Fereidoun Rassoulzadegan has been a major contributor to the understanding of the importance of protists in marine pelagic food webs. In the spirit of his research, we consider here one aspect of microzooplankton ecology that, in our opinion, has been misunderstood: the capacity of protist herbivores to control initiation and development of mass phytoplankton blooms, with a focus on diatom blooms. We argue that microzooplankton grazers probably cannot prevent bloom initiation and out-growth during mesotrophic to eutrophic conditions. We base our contention on the propositions that (1) mass diatom blooms do, in fact, routinely occur in the ocean at all latitudes; (2) since prey abundance is a main factor controlling protist growth, the grazing impact of herbivorous protists will be minor in the early stages of a bloom when prey abundances and, therefore, protist growth rates, are low; (3) due to food limitation during pre-bloom conditions, protist biomass will usually be low at the onset of a bloom, which serves to limit initial grazing impact; and (4) biomass of herbivorous protists is ultimately top-down controlled, thus curtailing the potential for microzooplankton to grow to sufficient abundance to graze down a developed bloom. We conclude that herbivorous protists are not likely to be able to prevent the initiation and development of mass blooms when conditions are favorable for rapid phytoplankton growth.

KEY WORDS: Microzooplankton · Ciliates · Heterotrophic dinoflagellates · Herbivory · Diatoms · Phytoplankton blooms · Plankton ecology

INTRODUCTION

The potential grazing impact of microzooplanktonic protists on phytoplankton production and standing stocks has been considered over the years by a variety of plankton ecologists (Rassoulzadegan & Etienne 1981, Banse 1982, 1992, Sherr & Sherr 2002, Strom 2002, Calbet & Landry 2004, Irigoien et al. 2005). That herbivorous protists, including ciliates and heterotrophic dinoflagellates, regularly consume a significant fraction of phytoplankton standing stocks and biomass production in the ocean is indisputable (Strom et al. 2001, Calbet & Landry 2004, Strom et al. 2007, Calbet 2008, Landry et al. 2008). In this review, we examine the concept that protist grazers can control, or even prevent, initiation and subsequent out-growth of phytoplankton blooms. Phytoplankton blooms, defined as a rapid and significant increase above the prevailing background in cell abundance or of chlorophyll *a* (chl *a*) as a proxy for biomass of photosynthetic plankton, occur at various scales in all regions of the sea (Legendre 1990, Cloern 1996, McGillicuddy et al. 2007, Wilson & Qiu 2008). Here we focus on the role of microzooplankton in limiting development of blooms, notably diatom blooms, which occur during meso- to eutrophic conditions of nutrient and light levels that are conducive to maximum rates of phytoplankton cell growth.

The idea that microzooplankton can limit bloom initiation has been expressed in a number of publications.

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Strom & Morello (1998, p. 582) wrote that 'Considering maximum growth rates alone, ciliates should be better able than dinoflagellates to control incipient blooms of their prey.' In a review of the interactions between microzooplankton grazers and phytoplankton, Tillmann (2004, p. 156) stated 'if community grazing controls initial stages of bloom development, there simply is no bloom.' Irigoien et al. (2005) proposed a 'loophole' hypothesis for phytoplankton blooms in which 'blooming species are those able to escape control by microzooplankton through a combination of predation avoidance mechanisms (larger size, colonies, spines, and toxic compounds) at the beginning of the bloom.' Rose & Caron (2007) hypothesized that temperature constraint on the maximum growth rates of herbivorous microzooplankton is a major factor in the initiation and development of mass blooms of phytoplankton in high latitude, cold water regions of the ocean.

The concept that microzooplankton could have the capacity to control bloom formation stems from the following facts: (1) microzooplankton are more significant than metazooplankton grazers as consumers of phytoplankton biomass and production (Calbet & Landry 2004, Calbet 2008); and (2) protistan grazers are capable of growing as fast as their phytoplankton prey (Sherr & Sherr 1994, Strom & Morello 1998). In both low nutrient oligotrophic and high nutrient-low chlorophyll (HNLC) regions of the sea, where the phytoplankton community is dominated by cells <10 µm in size, it is generally accepted that grazing by herbivorous protists consumes much of the daily phytoplankton production, minimizing potential for blooms and leading to seasonal stability in phytoplankton stocks (Miller et al. 1991, Banse 1992, Strom et al. 2000, Calbet & Landry 2004). More recent information that microzooplankton grazers, especially heterotrophic dinoflagellates, are also dominant consumers of larger-sized algae such as bloom-forming diatoms (reviewed in Sherr & Sherr 2007; Fig. 1) has highlighted the potential role of protists as grazers of blooms during meso- to eutrophic conditions.

Banse (1982) was the first to examine the theoretical potential for microzooplanktonic protists to graze phytoplankton stocks and production, although his review was limited to ciliates. Here we update the conclusions of Banse (1982) that, although herbivorous protists have high intrinsic growth rates, their *in situ* abundance and growth rates are low due to food limitation, and that top-down control could limit the capacity of herbivorous protists to control phytoplankton blooms. We expand Banse's (1982) analysis to include both ciliates and heterotrophic dinoflagellates. Our intent is to show that even though microzooplankton may indeed be able to limit small-scale blooms of phytoplankton <10 µm in size under generally oligotrophic conditions, protist grazers cannot control the initiation and development of mass phytoplankton blooms under meso- and eutrophic conditions, and may have a limited role in constraining maximum bloom biomass. The toxic and mechanical properties of some bloom-forming phytoplankton proposed by Irigoien et al. (2005) and temperature constraints on protist growth rates proposed by Rose & Caron (2007) undoubtedly are factors in the reduced grazing response of herbivorous protists. However, other important factors, originally suggested by Banse (1982) for ciliates and emphasized here, are the grazing and growth responses of marine phagotrophic protists to prey biomass, the routinely low standing stocks of protists during non-bloom conditions, and the top-down control of ciliates and heterotrophic dinoflagellates by predators.

PHYTOPLANKTON BLOOMS IN OCEAN ECOSYSTEMS

Satellite ocean color data has yielded detailed information on the temporal and spatial distribution of the higher chl *a* concentrations indicative of blooms (e.g. Doney et al. 2003, Wilson & Qiu 2008). In oligotrophic open ocean gyres, blooms are generally minor, of limited duration, and dominated by small-sized cells. However, an important part of total marine primary production is due to mass phytoplankton blooms dominated by the large-sized and chain-forming species of diatoms which characterize spring and upwelling blooms (Sarthou et al. 2005, Barber & Hiscock 2006). Large-sized diatoms also dominate blooms induced by experimental addition of iron in HNLC regions of the sea (Saito et al. 2006, Barber & Hiscock 2006) and those episodically observed as a consequence of eddy-driven upwelling (Falkowski et al. 1991, McGillicuddy et al. 2007, Brown et al. 2008). Marine diatom blooms are responsible for most export production, which is significant in terms of both organic sinking flux and food webs supporting marine fisheries (Iverson 1990, Barber & Hiscock 2006). Understanding potential controls and fates of such mass blooms is also of central importance in evaluation of the potential of marine systems to sequester atmospheric carbon dioxide as a result of the export of organic matter to the subsurface ocean (Longhurst 1991, Emerson & Hedges 2009).

Rose & Caron (2007) suggested that the occurrence of mass phytoplankton blooms in high latitude marine systems could be due to failure of herbivorous microzooplankton to grow quickly enough at low water temperatures (<~5°C) and thus control bloom formation. However, mass blooms, mainly of diatoms, occur at all latitudes in the ocean, not only in polar and subpolar regions (examples given in Table 1). Spring diatom

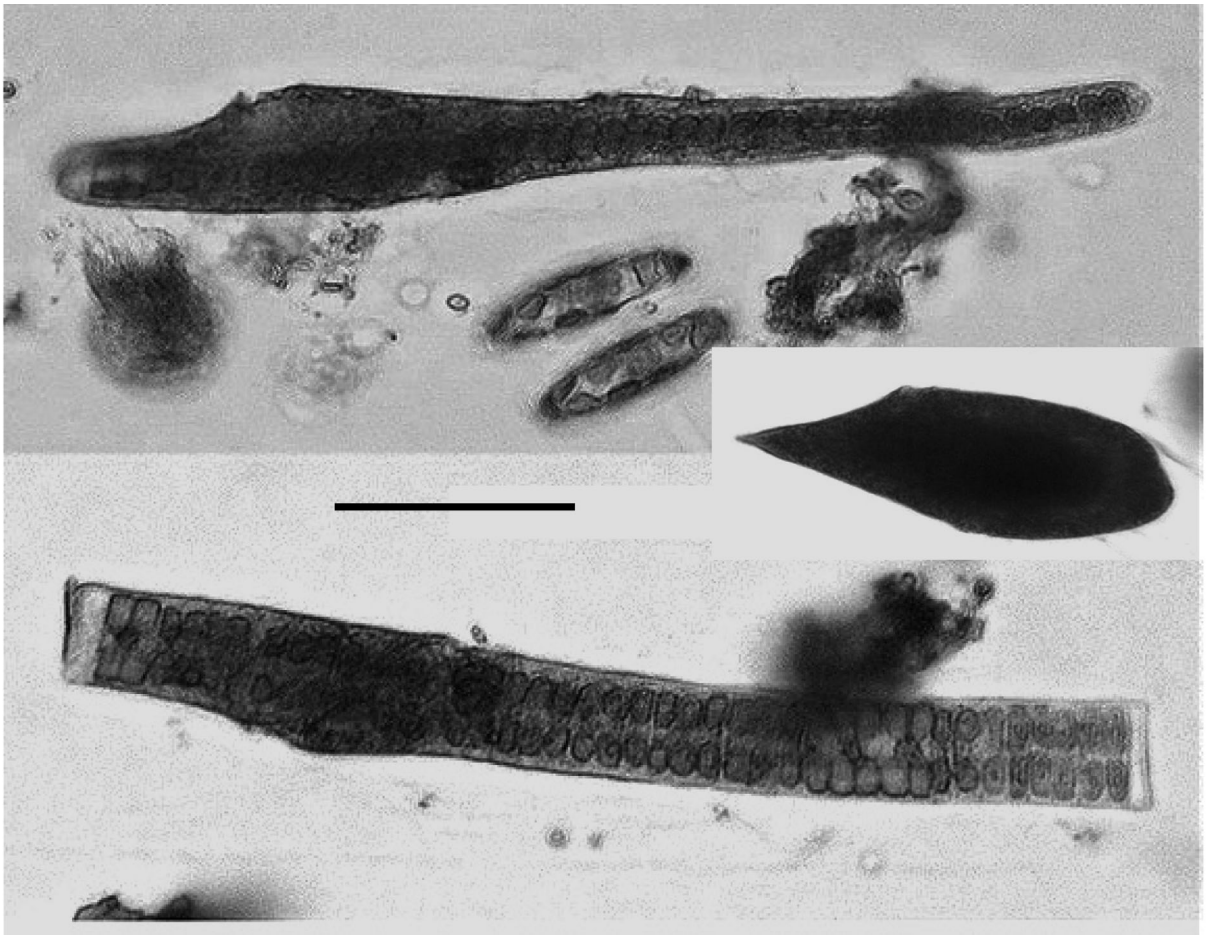

Fig. 1. *Gyrodinium* sp. with an ingested diatom chain much longer than the usual cell length of the dinoflagellate. Two separate images of the same heterotrophic dinoflagellate cell are shown. Inset image is of a similar *Gyrodinium* sp. cell without obvious ingested prey. The dinoflagellates were in a sample collected from the upper water column of the Bering Sea, 59.2° N 175.9° W, in April 2008 during a spring diatom bloom. Samples for microzooplankton analysis were preserved with 5% acid Lugol's solution, and individual protists visualized and sized using an image analysis system consisting of a Cooke Sensicam QE CCD camera with Image Pro Plus software, mated to an Olympus BX61 microscope. Scale bar = 50 µm. Other images of heterotrophic gymnodinoid dinoflagellates with ingested diatoms are in Strom & Strom (1996) and Calbet (2008) and available at http://bioloc.coas.oregonstate.edu/SherrLab/Microplankton%20images.html

blooms are a major seasonal feature of ocean biology in both temperate and high-latitude ecosystems. Upwelling-induced diatom blooms occur in temperate to tropical regions where surface water temperatures can be >15°C during bloom development (Table 1). Water temperature does not appear to be a universally important factor in accumulation of high diatom biomass when nutrients and light are not limiting to phytoplankton growth.

RELATION OF MICROZOOPLANKTONIC PROTIST GROWTH RATES TO FOOD CONCENTRATION

That grazing and growth rates of marine herbivorous ciliates and dinoflagellates are related to prey abundance by hyperbolic functions analogous to that of Michaelis-Menten kinetics has long been known and is well documented in the literature (Table 2). Virtually all species-specific response data for marine phagotrophic protists have been derived from laboratory culture experiments. A problem with such laboratory experiments is that abundances of algal prey offered to the protists are often much higher than natural phytoplankton concentrations. *In situ* food concentrations for herbivorous protists are in the range of 10s to 100s of µgC l^{-1}, or 10^3 to 10^4 algal cells ml^{-1}, even in eutrophic systems. In terms of chl *a*, marine phytoplankton stocks are generally <0.5 µg chl *a* l^{-1} under oligotrophic conditions, 0.5 to 5 µg chl *a* l^{-1} in mesotrophic conditions, and >5 µg chl *a* l^{-1} during eutrophic blooms (Li 2002, Sherr et al. 2006, Wilson & Qiu 2008). Data on phyto-

Table 1. Examples of published reports of mass phytoplankton blooms observed *in situ* in various regions of the world's oceans

Location	Surface water temperature (°C)	Bloom description	Maximum chl *a* (µg l^{-1})	Source
Polar				
Borge Bay, Antarctic	0.5–1.6	Mixed >20 µm size diatoms	11–39	Clarke & Leakey (1996)
Ross Sea, Antarctica	<2	Mixed diatoms/*Phaeocystis*	3–13.5	Smith et al. (2000)
South Georgia, Anarctica	3.2	Mixed diatoms	19	Atkinson et al. (1996)
Western Arctic Ocean	–1–6	Mixed diatoms	7–18	Sherr et al. (2009)
Temperate				
Dutch coast, North Sea	7–15	Mixed diatoms/*Phaeocystis*	10–43	Peperzak et al. (1998)
Ria de Vigo, NW Spain	15–21	Mixed diatoms	17.5–22.2	Moncoiffe et al. (2000)
Oregon upwelling	9–11	Mixed diatoms	20–43	Sherr et al. (2006)
Peruvian upwelling	15–16	Mixed diatoms	20–45	Bruland et al. (2005)
Chilean upwelling	16–17	Mixed diatoms	13–18	Escribano & Hidalgo (2000)
Tropical /subtropical				
Baja California upwelling	14–17	Mixed diatoms/dinoflagellates	12–18	Walsh et al. (1974)
Peruvian upwelling	16–17	Mixed diatoms	4–10	DiTullio et al. (2005)

plankton and microzooplankton biomass — binned into oligotrophic, mesotrophic, and eutrophic states — combined for samples collected in the California Current System, western Arctic Ocean, and Bering Sea are presented in Table 3. Similar ranges of phytoplankton and protist biomass have been found in other oceanic regions (Li 2002, Irigoien et al. 2004).

We drew data from a number of studies of the growth rates of marine ciliates and heterotrophic dinoflagellates fed algal prey over a range of concentrations that included, at the lower end, algal abundances characteristic of *in situ* levels. We used the empirical equation provided in each paper that described protist growth rate as a function of prey abundance or biomass to calculate the concentrations of algal prey at which growth was zero, 50% of μ_{max} (maximum specific growth rate), and 90% of μ_{max}. Prey concentrations that yielded these growth rates were converted from units of algal abundance or carbon biomass per volume presented by the authors to equivalent concentrations of chl *a*, based on data given in the papers and/or an assumed conversion factor of 50 µgC µg chl a^{-1}. The algal concentration that corresponded to the higher growth rate, 90% of μ_{max}, was selected since these hyperbolic functions approach μ_{max} only at extremely high prey abundance. These data showed a wide range in species-specific growth responses to food concentration (Table 2). With exception of outliers, the threshold concentration for growth was between 0.1 and 2 µg chl *a* l^{-1}. Growth rates equivalent to 50% of μ_{max} occurred at chl *a* concentrations ranging from 0.25 to 5 µg l^{-1}. The herbivorous protists did not attain 90% of their μ_{max} until prey biomass reached levels equivalent to 1 to >100 µg chl *a* l^{-1}, with most of the protists requiring algal concentrations >5 µg chl *a* l^{-1} for near-maximum growth rates. These data suggest that most phagotrophic protists would have negligible growth rates under low chl *a* concentrations, and only grow at rates near their intrinsic μ_{max} when phytoplankton stocks were at levels characteristic of a developed bloom.

Microzooplankton grazing would thus be unlikely to be able to prevent the initiation of a phytoplankton bloom due in part to the disparity in growth rates of phytoplankton and herbivorous protists in the early stages of a bloom. At the beginning of a bloom, when phytoplankton biomass is low, algal cells grow at the maximum rate at which nutrient supply, light, and temperature allow. Since the growth rate of herbivorous protists is related to prey biomass by responses in which growth is much less than μ_{max} at low food abundance, herbivorous protists would grow slowly at the onset of a bloom. Only after a bloom had developed and food abundance was non-limiting could herbivorous microzoooplankton approach their maximum growth rates.

LOW STANDING STOCKS OF HERBIVOROUS PROTISTS WHEN PHYTOPLANKTON BIOMASS IS LOW

Ciliates and heterotrophic dinoflagellates are routinely observed in ocean waters characterized by low chl *a* concentrations, but generally at low biomass, <10 µgC l^{-1} (Irigoien et al. 2004; our Table 3). A low initial stock of protistan predators, combined with low protist growth rates and the possibility of low cell-specific metabolism at the beginning of a bloom, would further preclude control of bloom formation by microzooplankton. An empirical example of how phytoplankton blooms can develop in the presence of micro-

Table 2. Published growth rate responses to prey abundance for species of herbivorous ciliates and dinoflagellates. Empirical equations provided in each paper describing protist growth rate as a function of prey abundance were used to calculate chlorophyll *a* (chl *a*) concentrations below which growth cannot be sustained (threshold for growth), and chl *a* concentrations at which protist growth rate would be approximately 50 and 90% of maximum growth rate (μ_{max}). Chl *a* values were estimated from abundance or carbon per unit volume data presented in the papers, assuming a C:chl *a* ratio of 50:1. nd: not determined

Protist species	Cell size (μm^3)	Algal prey	Growth temp. (°C)	μ_{max} (d^{-1})	Chl *a* conc. (µg chl *a* l^{-1}) Threshold	50% μ_{max}	90% μ_{max}	Source
Ciliates								
Balanion comatum	2500	*Rhodomonas salina*	15	1.39	0.18	0.25	0.80	Jakobsen & Hansen (1997)
Amphorides quadrilineata	nd	*Isochrysis galbana*	21	0.38	0.5	1.0	5.5	Jakobsen et al. (2001)
Lohmaniella uniformis	3800	*Nephroselmis pyriformis*	12.5	0.50	0.68	2.0	13.5	Gismervik (2005)
Strombidium vestitum	8200	*N. pyriformis*	11	1.04	0.13	0.72	5.7	Gismervik (2005)
Strombilidium veniliae	19600	*Choomonas salina + I. galbana*	16	0.73	2.0	nd	28	Montagnes (1996)
Strombidium sp.	28400	*N. pyriformis*	12.5	0.80	0.48	2.3	16	Gismervik (2005)
Strombidium sirculum	28600	*Thalassiosira pseudonana*	16	0.57	0.32	1.0	6.8	Montagnes (1996)
Strombidium acutum	28700	*N. pyriformis*	11	0.55	0.47	1.0	5.1	Gismervik (2005)
Strombidium conicum	38300	*N. pyriformis*	11	0.63	0.13	0.35	2.2	Gismervik (2005)
Strombidium reticulatum	40000	*Pyramimonas* sp.	12	0.84	0.28	2.3	19	Jonsson (1986)
Strombidium capitatum	64100	*C. salina + I. galbana*	16	1.07	5.4	13.6	65	Montagnes (1996)
Strombidium spiralis	68450	*N. pyriformis + Hemiselmis* sp.	15	1.52	0.40	1.2	8.1	Gismervik (2005)
Strobilidium neptuni	110000	*C. salina*	16	1.84	8.0	nd	68	Montagnes (1996)
Lohmaniella spiralis (*Strombidium spiralis*)	150000	*Pyramimonas* sp.	12	1.12	0.23	1.9	16	Jonsson (1986)
Strombidinopsis multiauris	186000	*Gymnodinium simplex*	15	0.75	1.6	3.5	28	Montagnes & Lessard (1999)
Strombidinopsis sp.	560000	*Prorocentrum minimum*	19	1.06	0.30	1.1	7.6	Jeong et al. (1999)
Strombidinopsis sp.	560000	*Scrippsiella troichoidea*	19	0.67	0.58	1.8	12	Jeong et al. (1999)
Strombidinopsis sp.	560000	*Gymnodinium sanquineum*	19	1.27	0.24	1.0	7.4	Jeong et al. (1999)
Thecate heterotrophic dinoflagellates								
Protoperidinium bipes	1200	*Skeletonema costatum*	20	1.37	2.2	10.4	80	Jeong et al. (2004)
Oblea rotunda	5500	*Ditylum brightwellii*	20	0.66	0.20	1.5	3.0	Strom & Buskey (1993)
Protoperidinium excentricum	24000	*Ditylum brightwellii*	12	0.35	0.12	0.82	6.4	Menden-Deuer et al. (2005)
Protoperidinium pellucidum	24600	*Thalassiosira* sp.	20	0.80	0.20	1.0	7.4	Buskey (1997)
Protoperidinium conicum	50000	*Ditylum brightwellii*	12	1.20	0.0	0.6	1.1	Menden-Deuer et al. (2005)
Protoperidinium cf. *divergens*	119000	*Gonyaulax polyhedra*	20-23	0.50	0.0	24	120	Jeong & Latz (1994)
Protoperidinium crassipes	204000	*G. polyhedra*	20-23	0.33	0.0	12	108	Jeong & Latz (1994)
Athecate heterotrophic dinoflagellates								
Gymnodinium sp.	160	*R. salina*	15	0.92	0.28	0.66	0.96	Jakobsen & Hansen (1997)
Gymnodinium sp.	1000	*I. galbana + Synechococcus* sp.	13	0.84	0	0.40	3.6	Strom (1991)
Gyrodinium dominans	1200	*P. minimum*	20	1.13	0.29	0.66	3.6	Kim & Jeong (2004)
Gymnodinium cf. *perparvum*	1700	Mixed phytoflagellates	1	0.30	0.0	1.0	8.8	Bjørnsen & Kuparinen (1991)
Gyrodinium spirale	11500	*Heterocapsa triqueta*	15	0.60	0.28	18	67	Hansen (1992)
Gyrodinium spirale	13000	*P. minimum*	20	0.79	0.46	1.9	14	Kim & Jeong (2004)

Table 3. Summary of data sets on total microzooplankton protist (MZP) biomass and fraction of total MZP biomass composed of heterotrophic dinoflagellates, compared to chlorophyll *a* (chl *a*) concentrations from the California Current System (CCS) off Oregon (2002–2003, 106 samples collected at stations described in Sherr et al. 2005), the western Arctic Ocean (2002–2006, 58 samples described in Sherr et al. 2009 and C. J. Ashjian et al. unpubl. data), and the Bering Sea (spring 2008, 18 samples). MZP biomass was determined from Utermohl analysis of abundance and cell biovolume of ciliates and heterotrophic dinoflagellates in samples preserved in 5 or 10% acid Lugol's solution (Sherr et al. 2009). Carbon biomass of protists was calculated based on a C:biovolume factor of 0.19 pgC μm^{-3} (Putt & Stoecker 1989) for ciliates and on the C:biovolume algorithm for heterotrophic protists of Menden-Deuer & Lessard (2000) for dinoflagellates. Chl *a* concentration was determined fluorometrically (Sherr et al. 2005, 2009). Data were binned into 3 groups based on trophic states defined by ranges of chl *a* concentration: oligotrophic, mesotrophic, and eutrophic. Higher chl *a* concentrations in all regions sampled were due to mixed-species diatom blooms. Phytoplankton composition in the CCS and western Arctic Ocean is described in Sherr et al. (2005, 2009), respectively. Phytoplankton biomass was estimated from chl *a* values using C:chl *a* values of 60, 50, and 40 for oligotrophic, mesotrophic, and eutrophic conditions, respectively. Values are means ± 1 SD (range)

Trophic state	Chl *a* ($\mu g\ l^{-1}$)	Phytoplankton biomass ($\mu g\ l^{-1}$)	MZP biomass $\mu g\ l^{-1}$	Phytoplankton/ MZP biomass ratio	Heterotrophic dinoflagellate fraction of total MZP biomass
Oligotrophic <0.5 µg chl *a* l^{-1}	0.30 ± 0.10 (0.14–0.48)	17.7 ± 6.2 (8.4–29)	8.1 ± 5.5 (1.6–27)	3.3 ± 2.8 (0.34–13)	0.65 ± 0.19 (0.22–0.99)
Mesotrophic 0.5–5 µg chl *a* l^{-1}	1.2 ± 1.1 (0.55–4.8)	59 ± 53 (28–238)	14.4 ± 15.0 (1.5–91)	6.5 ± 7.1 (0.5-52)	0.63 ± 0.23 (0.10–0.99)
Eutrophic >5 µg chl *a* l^{-1}	13.0 ± 8.12 (5.1–43)	520 ± 330 (200–1720)	24.5 ± 20.9 (1.9–106)	40 ± 44 (2–240)	0.64 ± 0.21 (0.23–0.94)

zooplankton grazers is presented by Suffrian et al. (2008). They followed change in biomass of both phytoplankton (mainly diatoms) and microzooplankton (ciliates and heterotrophic dinoflagellates), as well as grazing impact of microzooplankton, during the course of nutrient-stimulated blooms in mesocosms in a Norwegian fjord with an *in situ* water temperature of 10°C. Their results showed that microzooplankton grazers were not able to inhibit bloom initiation or development as a consequence of low initial protist abundance. The biomass of herbivorous protists was <24 µgC l^{-1} at the beginning of the mesocosm bloom, and only attained maximum values (90 to 130 µgC l^{-1}, dominated by *Gyrodinium* sp. dinoflagellates) after the peak of the bloom.

A problem associated with the low standing stocks of microzooplankton is the issue of survival and persistence of herbivorous protists at *in situ* chl *a* concentrations for which protist growth is negligible (Table 2). Understanding how protists capable of grazing bloom-forming phytoplankton, particularly diatoms, survive between blooms is critical to understanding the ability of these protists to respond when blooms recur. The question of persistence of herbivores in the plankton has been previously addressed by Strom et al. (2000) and Paffenhofer et al. (2007). In culture, survival of marine ciliates is sensitive to the prey threshold for growth. Montagnes (1996) found rapid mortality of 4 marine oligotrich ciliates at sub-threshold concentrations of algal prey, and theorized that herbivorous ciliates could only survive in oligotrophic conditions by exploiting small-scale patches of phytoplankton. The idea that small-scale patches of higher prey abundance are key to survival of both meso- and microzooplankton when bulk chl *a* levels are low is supported in the review of Paffenhofer et al. (2007).

Other possibilities for persistence of protists at low prey abundance are sequestration of chloroplasts by mixotrophic ciliates as a food resource (Stoecker 1991, Stoecker et al. 2009, this Special Issue) or feeding on alternate prey such as bacteria or other heterotrophic protists (Sherr et al. 1989, Bernard & Rassoulzadegan 1990, Verity 1991, Jeong et al. 2004, 2007). Individual species of heterotrophic dinoflagellates have been found to survive at low prey abundance for periods of 2 to 71 d (Hansen 1992, Jakobsen & Hansen 1997, Menden-Deuer et al. 2005). Both ciliates and dinoflagellates may adapt to starvation by reducing their metabolic rate (Fenchel & Finlay 1983, Menden-Deuer et al. 2005).

TOP-DOWN CONTROL OF MICROZOOPLANKTON BIOMASS

Even if they cannot prevent initiation of a bloom, microzooplankton should have the capacity to affect phytoplankton biomass in the later stages of a bloom when growth rates of protist herbivores are not severely limited by prey abundance. However, the

potential for microzooplankton to curtail bloom biomass is likely constrained in natural systems due to top-down control (Smetacek 1981, Tillmann 2004, Calbet & Saiz 2005, Irigoien et al. 2004). The upper limit of microzooplankton biomass in eutrophic marine systems is lower than would be expected if herbivorous protists were able to graze down a significant portion of a developed bloom. For example, if protists were able to consume bloom biomass equivalent to 10 µg chl *a* l^{-1}, or 500 µgC l^{-1} assuming a C:chl *a* ratio of 50, with a growth efficiency of 40%, then a final microzooplankton biomass of 200 µgC l^{-1} would be expected. *In situ* microzooplankton biomass is usually well below that amount. Irigoien et al. (2004) compared data on global diversity and biomass of marine phytoplankton, microzooplankton, and mesozooplankton, and suggested that microzooplankton biomass rarely exceeded ~50 µgC l^{-1} and was not strongly correlated to chl *a* concentration due to predation by mesozooplankton.

A smaller data set from the California Current System off Oregon, USA, and from Arctic and sub-Arctic systems (authors' unpubl. data) also showed no significant relation between microzooplankton biomass and chl *a* concentration, with maximum biomass of herbivorous protists capped at ~50 to 100 µgC l^{-1} (Table 3). In our data set, ratios of phytoplankton to microzooplankton biomass were 3.3 ± 2.8 for oligotrophic conditions, 6.5 ± 7.1 for mesotrophic conditions, and 40 ± 44 for eutrophic conditions (Table 3). Such increasing ratios suggest limitation of microzooplankton biomass during and after bloom peaks. Phytoplankton blooms may be grazed down to some extent by microzooplankton, as described by Tillmann (2004) for coastal blooms of single-cell *Phaeocystis* sp., and by Saito et al. (2006) and Suffrian et al. (2008) for a nutrient-stimulated diatom blooms, if protist biomass is not strongly top-down controlled.

Marine ciliates and heterotrophic dinoflagellates are known to be a food resource for metazooplankton, although this depends on predator species and the relative abundances of protist and algal prey (reviewed in Stoecker & Capuzzo 1990, Calbet & Saiz 2005, Sherr & Sherr 2007, Campbell et al. 2009). Calbet & Saiz (2005) concluded that ciliates composed about 22 to 25% of the diet of copepods even in meso- to eutrophic systems in which phytoplankton abundances were 50 to >500 µgC l^{-1}. They acknowledged that the consumption of microzooplankton by copepods would be even greater if heterotrophic dinoflagellates were also included in these estimates. Based on the data presented in Table 3, heterotrophic dinoflagellates compose a variable but often high fraction of total biomass of microzooplanktonic protists, on average 63 to 65% under all trophic conditions. Calbet & Saiz (2005) and Sherr & Sherr (2007) noted several studies reporting that copepods selectively fed on heterotrophic dinoflagellates as well as on ciliates. Castellani et al. (2008) also found that the ingestion of microzooplankton by nauplii and adult females of *Calanus finmarchicus* and adult females of *Oithona similaris* was positively related to protist biomass, although ciliates composed a larger proportion of their diet compared to heterotrophic dinoflagellates. In the western Arctic Ocean, copepods showed selective preferences for microzooplankton protists compared to phytoplankton as food, based both on individual copepod species and the relative proportions of phytoplankton and heterotrophic protist biomass available (Campbell et al. 2009).

However, field evidence that microzooplankton stocks are actually depleted by copepods and other metazooplankton is not compelling. During the spring bloom season in the Celtic Sea, copepods removed 12 to 17% of the ciliate and heterotrophic dinoflagellate stocks pre-bloom, but only 2% of microzooplankton biomass at the peak of the bloom (Fileman et al. 2007). Castellani et al. (2008, p. 1095) had similar results in the Irminger Sea in the North Atlantic, reporting that 'Copepod grazing impact on total and on ciliates/dinoflagellates standing stock was < 0.5% and < 2%, respectively.'

There is undoubtedly additional consumption of herbivorous protists by other protists, although this trophic link is not well documented. A spirotrichous ciliate was shown to feed on heterotrophic dinoflagellates (Jeong et al. 2004), and both mixotrophic and thecate heterotrophic dinoflagellates are known to prey on marine ciliates (Bockstahler & Coats 1993, Jacobson & Anderson 1996, Uchida et al. 1997, Smalley et al. 1999). The impact of predation on microzooplanktonic protists by other protists is in need of further investigation.

Other factors may also limit protist abundance during blooms, including allelopathic chemicals produced by phytoplankton which act to inhibit protist feeding and growth, as suggested by Tillmann (2004) and Irigoien et al. (2005). The best documented case of chemical deterrence of protist grazing is that by dimethylsulfoniopropionate-producing algae, e.g. the coccolithophorid *Emiliania huxleyi* (Wolfe 2000, Strom et al. 2003, Strom 2008). Some species of marine diatoms produce polyunsaturated aldehydes (PUAs) which inhibit reproduction in copepods (Miralto et al. 1999, Ribalet et al. 2007, Wichard et al. 2007). Whether diatom PUAs also affect grazing or growth of herbivorous protists is currently unknown. Harmful algal bloom (HAB) phytoplankton, which include many species of autotrophic dinoflagellates, regularly form dense blooms which may reduce grazing mortality due to toxins produced by the algae (Turner & Tester 1997).

However, some species of herbivorous protists have been shown to ingest and grow on selected species of HAB phytoplankton (Jeong & Latz 1994, Jeong et al. 2002, Calbet et al. 2003, Johnson et al. 2003, Kim & Jeong 2004). The lack of critical information about the predator–prey interactions between microzooplanktonic protists and bloom-forming algae hinders accurate modeling of marine planktonic food webs and elemental fluxes.

CONCLUSIONS

While microzooplankton are certainly able to consume a substantial fraction of marine phytoplankton production under both bloom and non-bloom conditions, we conclude the following regarding the capacity of herbivorous protists to impact the development of mass phytoplankton blooms:

(1) The fact that mass phytoplankton blooms, notably diatom blooms, routinely occur at all latitudes in the sea suggests that neither metazooplankton nor microzooplankton herbivores are able to prevent the initiation, or significantly impede the development, of such blooms.

(2) At the onset of a bloom, herbivorous protist stocks and grazing rates would probably not be sufficiently high to suppress bloom formation, due in large part to low protist growth rates at low prey concentrations.

(3) Maximum abundance and biomass of herbivorous protists are likely top-down controlled by predation and possibly other factors (e.g. allelopathic inhibition of grazing) during blooms, so that protists may not be able to attain abundance levels required to graze down a bloom after it forms. The upper limit of microzooplankton biomass in marine systems appears to be on the order of 50 to 100 µgC l^{-1}.

As Calbet (2008) noted, more work is needed on the distribution and ecology of marine microzooplankton, including both ciliates and heterotrophic dinoflagellates, in particular on feeding and growth rates at natural prey abundances and temperatures, and on the processes limiting maximum microzooplankton biomass *in situ*. Such data would provide information crucial to adequately parameterize models of planktonic food webs.

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