REVIEW ARTICLE

From small scales to the big picture: persistence mechanisms of planktonic grazers in the oligotrophic ocean

Gustav-Adolf Paffenhöfer[1], Barry F. Sherr[2] & Evelyn B. Sherr[2]

1 Skidaway Institute of Oceanography, Savannah, GA, USA
2 College of Oceanic & Atmospheric Sciences, Oregon State University, Corvallis, OR, USA

Abstract

In this review we evaluate whether universal behavioral and metabolic mechanisms exist, which permit marine proto- and metazooplankton to persist in continuously food-limited environments such as the North Pacific Subtropical Gyre and other oligotrophic ocean systems. We re-visit the issue of what processes account for low steady-state abundance of the dominant groups of planktonic grazers: phagotrophic protists and copepods, by examining evidence for the four processes proposed by Strom *et al.* (2000): grazing thresholds, behavioral response to prey patchiness, top–down control of grazers, and mixotrophy (combination of photosynthesis and phagotrophy in protists) and/or omnivory (switching between alternate prey types). Published observations reveal that grazing thresholds, below which feeders reduce their feeding efforts and, with that, their metabolic expenditures, do exist. There are also studies suggesting that both protistan and small metazoan plankton feeders may take advantage of patchiness of food particles and are frequently mixotrophic and/or omnivorous. Predator patchiness in response to prey patches may facilitate top–down control of grazers. Finally, we discuss processes, which may lead to low quasi steady-state abundances of food particles and feeders.

Problem

It is well known that the epipelagic zone of oligotrophic open ocean ecosystems is characterized by low quasi-steady state abundances of microorganisms, including phytoplankton (Eppley *et al.* 1973; Miller *et al.* 1991; Caron *et al.* 1995; Webber & Roff 1995; Caron *et al.* 1999; Sherr *et al.* 2003; Teira *et al.* 2005), heterotrophic prokaryotes (Ducklow 2000; Landry & Kirchman 2002; Li *et al.* 2004) and phagotrophic protists (Boyd *et al.* 1995; Caron *et al.* 1995; Sherr *et al.* 2003) (Table 1). However, the controlling processes that maintain such steady-state abundances are not well understood, *i.e.* we do not understand why 'blooms and busts' in abundances of microbes seldom occur in the oligotrophic open ocean, and why prey concentrations do not drop to zero.

With respect to the case of the high nutrient low chlorophyll (HNLC) region of the North Pacific Gyre (Miller *et al.* 1991), Strom *et al.* (2000) considered processes that might be responsible for sustained low microbial abundances and low standing stock variability – *i.e.* which factors might lead to such stability. Based on the analysis of various models and on the lack of sufficient empirical information they concluded that, to date, no convincing explanation existed as to how chlorophyll biomass is controlled in HNLC regions. Strom *et al.* (2000) evaluated four 'candidate explanations' affecting the persistently low chlorophyll values in the North Pacific. These included (i) grazing thresholds for the dominant herbivores, phagotrophic protists, although at the time this paper was published only one putative threshold had been reported *in situ* for microzooplank-

Table 1. Abundances of unicellular organisms, as biomass stocks and as chl *a* concentrations in the epipelagic zone of oligotrophic oceans.

Organism	Biomass μg C l^{-1}	Location	Reference
Prokaryotes			
Heterotrophic bacteria	5–30	Open ocean	Ducklow 2000
	3–23	NE Pacific Ocean, gyre	Sherr *et al.* (2006)
Total bacteria	2–8	Sargasso Sea August	Caron *et al.* (1999)
Total prokaryotes	7–20	Tropical Pacific	Landry & Kirchman (2002)
Heterotrophic flagellates	3.6	Sargasso Sea, August	Caron *et al.* (1995)
Microplanktonic protists	0.9	Sargasso Sea, August	Caron *et al.* (1995)
	1.1	NE Atl Subtr Gyre	Quevedo *et al.* (2003)
Coccoid cyanobacteria + <5 μm eukaryotic algae	1–20	NE Pacific Ocean, gyre	Sherr *et al.* (2005)
Total nanoplankton	3–27	Sargasso Sea, August	Caron *et al.* (1995)
Total nanoplankton	3–18	N Atl Subtr Gyre	Paffenhöfer *et al.* (2003)
Phytoplankton biomass	μg Chl *a* l^{-1}		
Total chlorophyll	0.04–0.23	N Pacific Subtr. Gyre	Eppley *et al.* (1973)
Total chlorophyll	0.04–0.45	Sargasso Sea August	Caron *et al.* (1995)
	0.04–0.25	Sargasso Sea August	Caron *et al.* (1999)
Total chlorophyll	0.03–0.35	Caribbean Sea	Webber & Roff (1995)
Total chlorophyll	0.04–0.30	N Atl Subtr Gyre	Teira *et al.* (2005)
Total chlorophyll	0.3–0.4	Subarctic Pacific Ocean	Miller *et al.* (1991)

tonic protists (Lessard & Murrell 1998); (ii) prey patchiness, for which Strom *et al.* did not find convincing *in situ* data; (iii) carnivory, *i.e.* top–down control of protistan grazers by carnivores which the authors did not see as sufficiently robust to allow controlling minima and maxima of phytoplankton biomass; and (iv) multiple-prey and multi-predator activities, which would include switching among different prey types, depending on their respective abundance. This, Strom *et al.* thought, could provide the observed stability within prey communities. There is evidence of prey-switching among copepods (*e.g.* Landry 1981), as well as evidence for prey selection by phagotrophic protists offered two or more types of prey (Verity 1991a; Boenigk *et al.* 2002; Matz *et al.* 2002; Martel 2006). Strom *et al.* concluded 'An experimental focus on the physiological and behavioral capabilities of representative microherbivores will be required to make progress in this area.'

Here we re-visit the issue of what processes account for low steady-state abundance of the dominant groups of planktonic grazers: phagotrophic nanoflagellates, protists in the microplankton (mostly dinoflagellates and ciliates), and also copepods, by examining evidence for the four processes proposed by Strom *et al.* (2000). Based on a review of published data on feeding activities and rates of copepods at very low food levels, and of metabolic rates over time of phagotrophic protists and of copepods, plus data on sensory performance and *in situ* patchiness, we hypothesize that behavioral and metabolic responses of protists and copepods to changes in food abundance and

in types of prey are main factors contributing to the quasi steady-state abundances both of prey and of predators in oligotrophic, epipelagic marine environments.

Grazing Thresholds: Behavioral and Metabolic Responses of Planktonic Grazers Near Minimum Food Concentrations

According to Steele (1974), to maintain a degree of stability in plankton communities a reduction of feeding effort is essential once food abundances reach low levels. There exists no direct, *in situ*, evidence that planktonic grazers diminish their feeding effort when food resources are depleted to some low level. However, various experimental observations in which food was offered at *in situ* concentrations have suggested a reduction of grazing effort once a certain low food abundance was reached. Such observations range from those of Adams & Steele (1966) who offered environmental particle abundances to late stages of *Calanus finmarchicus*, to studies on protozooplankton feeding on phytoplankton (Lessard & Murrell 1998). For several of these studies, detailed information is presented below to elucidate the processes occurring when food abundances are diminished.

Response of copepods to low food abundance

During 4-h grazing experiments, Corner *et al.* (1972) (Fig. 1) found that both copepodid stage V and adult females of *Calanus helgolandicus* lowered their clearance
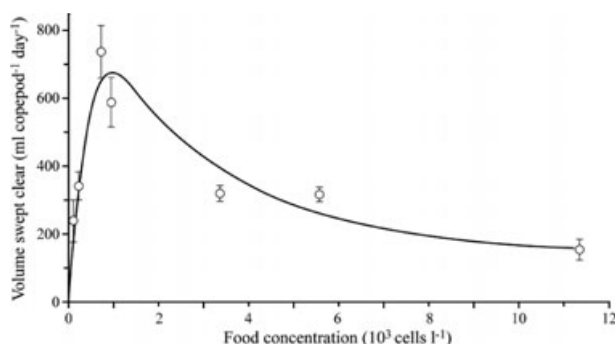
Fig. 1. *Calanus helgolandicus.* Feeding rate on the diatom *Biddulphia sinensis* in relation to food concentration (modified from Corner *et al.* 1972).

rates at food concentrations below 1000 cells l^{-1} (29 μg C l^{-1}) of *Biddulphia sinensis*. Using their experimentally determined assimilation efficiency of 34.1%, metabolic expenses were calculated according to equations from Ikeda (1985). It was found that while these copepods obtained sufficient food to cover their metabolic expenses at 29 μg C l^{-1} at the maximum clearance rate, ingesting 30.8% of their body carbon daily, at 15 μg C l^{-1} they ingested insufficient amounts to cover their metabolic needs (Table 2). Although these copepods had clearly reduced their feeding rate, they had not stopped feeding altogether! Similar observations were made for adult females of the large oceanic calanoid copepod *Eucalanus hyalinus elongatus* (Fig. 2, also Paffenhöfer 1988) feeding on the large diatom *Rhizosolenia alata*. *Eucalanus hyalinus / elongatus* has been found in the upper 500 m (Deevey & Brooks 1977) and between 50 and 100 m depth (Paffenhöfer & Mazzocchi 2003) of the Sargasso Sea. Here, too, the clearance rate increased with decreasing food concentration towards a maximum rate at a food level at which *E. hyalinus* obtained, at 90% assimilation efficiency (Paffenhöfer & Köster 2005), just sufficient amounts of food to support metabolic needs (Table 1). At food levels slightly lower than this, clearance rates dropped and ingestion barely covered 50% of the copepod's basic metabolic requirements (Table 2). Such
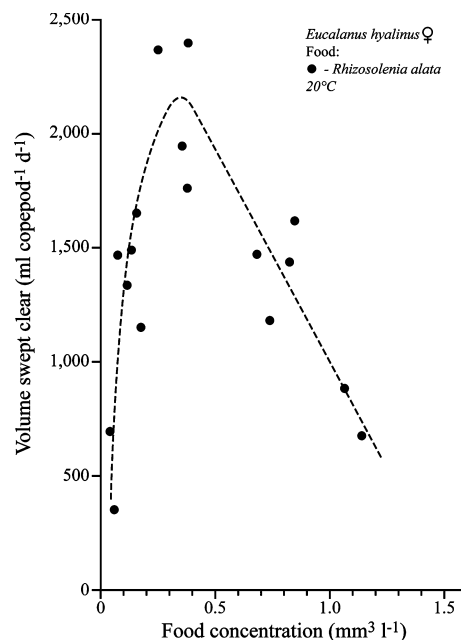

Fig. 2. Feeding rate of the calanoid *Eucalanus hyalinus* on the diatom *Rhizosolenia alata* (modified from Paffenhöfer 1988).

decreasing clearance rates have also been observed for copepods of the inshore/nearshore genus *Acartia* once lower food levels have been attained (Kiørboe *et al.* 1985; Paffenhöfer & Stearns 1988; Wlodarcyk *et al.* 1992).

How do copepods adjust their behavior as food concentrations drop below a certain threshold? Price & Paffenhöfer (1986) made visual observations of the behavioral response of *Eucalanus hyalinus* feeding on *Rhizosolenia alata*. *Eucalanus hyalinus* reached its maximum clearance rate at a diatom concentration of ~0.5 mm³ l^{-1}, moving its cephalic (feeding) appendages about 53% of the time (Price & Paffenhöfer 1986, Fig. 3). At a lower diatom concentration of *c.* 0.25 mm³ l^{-1}, the appendages moved only 38% of the time. The observed 28% decrease in movement of feeding appendages correlated with the 21% decrease in clearance rate between the higher to the lower prey concentrations. This implies that the copepod was expending less energy at the lower food

Table 2. Ingestion rates, metabolic expenditures and needs of two copepod species.

Species = Feeder & Food	Food conc (µg C l^{-1})	VSC (ml ♀$^{-1}$ day^{-1})	Ingestion[2]	Metabolic needs[1,2]	Need to ingest[2]
Calanus helgolandicus and *Biddulpia sinensis*	a. 29	680	30.8	5.2	16 at 34 %AE
Corner *et al.* (1972)	b. 15	470	10.5		
E. hyalinus and *Rhizosolenia alata*	a. 7.0	2150	8.8	7.0	8 at 90% AE
Paffenhöfer (1988)	b 3.4	1700	3.4		

VSC, volume swept clear; AE, assimilation efficiency; a., at maximum VSC; b., at half the food concentration of maximum VSC.
[1]Calculated from Ikeda (1985).
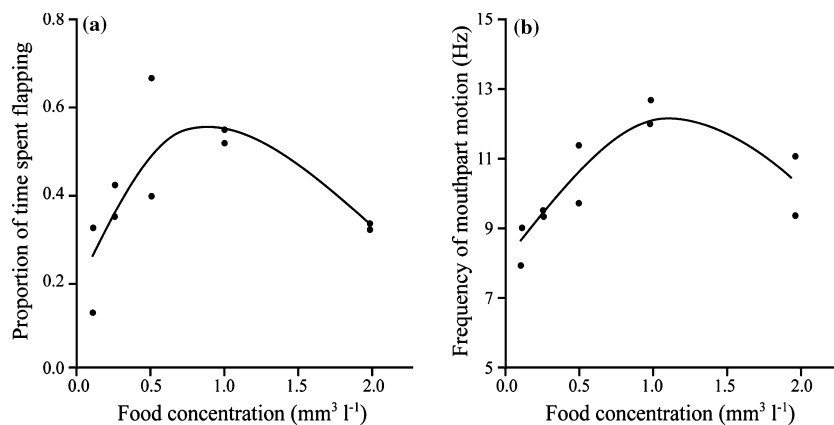[2]Expressed as percent of body carbon per day.

Fig. 3. Proportion of time moving cephalic appendages, and frequency of appendage movement of the calanoid *Eucalanus hyalinus/ elongatus* in relation to food abundance (modified from Price & Paffenhöfer 1986).

level. As food concentrations of *R. alata* decreased further, *E. hyalinus* spent even less time moving its appendages, and also reduced the frequency of motion. When food disappeared, *E. hyalinus* ceased appendage motion for days to weeks, remaining suspended in the water (8-l vessel) and moving the cephalic appendages only on rare occasions. Within minutes of adding a limited amount of *R. alata*, this copepod re-initiated feeding. *Eucalanus hyalinus* females appear to be capable of reducing their activity (presumably metabolism) substantially to survive more than 2 weeks at 20 °C without food. Fast-moving females of the calanoid copepod *Clausocalanus furcatus* have also been observed to reduce their motion velocity when food concentrations of the autotrophic dinoflagellate *Gymnodinium nelsoni* decreased from near 25 μg C l^{-1} to below 5 μg C l^{-1} over a period of 24 h. At the latter concentration they could not support their basic metabolic needs, which required an ingestion of about 27% of their body carbon per day (Paffenhöfer 2006).

Response of phagotrophic protists to low food abundance

Some protists are able to form specialized cells, termed cysts, which have very low metabolic rates and can persist for long periods of time; such species typically live in shallow-water environments where their cysts can rest in the sediment until conditions are conducive to excystment and renewed growth (Reid 1987; Caron *et al.* 1990; Strom 2002). Most planktonic protists in the open ocean do not form such resting cells. They are able, however to reduce their rate of metabolism, often dramatically, when they have stopped growing. Reduction in rate of respiration in starving compared with actively growing protists has been demonstrated in a number of laboratory experiments with isolated protistan species.

In one of the first such studies, Fenchel (1982a) observed reduction of metabolic expenditure by bacterivorous flagellates at low food availability, and a rapid
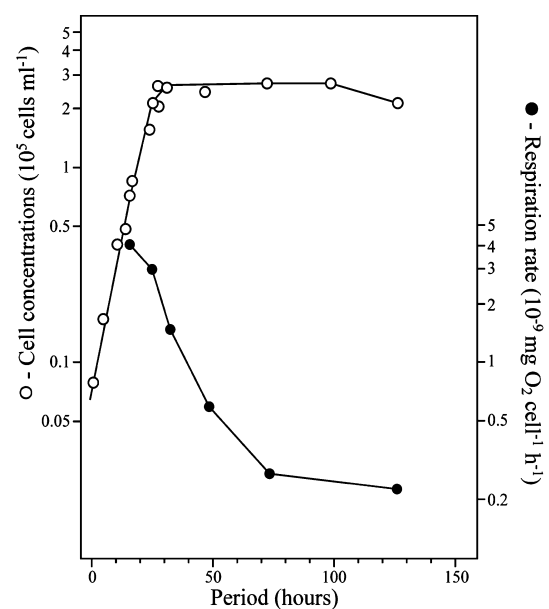

Fig. 4. Respiration rate and batch culture abundance of the nano-flagellate *Ochromonas* sp. (modified from Fenchel 1982a).

return to regular metabolism once food was again abundant. Near the exhaustion of bacterial food, the nanoflagellate *Ochromonas* sp. reduced its metabolic rate (rate of respiration) to only 5% of its regular rate 50 h after the onset of major food shortage (Fenchel 1982a, Fig. 4). Upon addition of bacteria at 2×10^8 ml^{-1}, those *Ochromonas* which had been without food for 25 h reached metabolic rates close to initial per cell rates within 1 h (Fig. 5). Caron *et al.* (1990) subsequently reviewed a range of comparable studies on respiration rates of growing *versus* starving bacterivorous flagellates and ciliates in culture. These data imply that in open-ocean systems, phagotrophic protists should be able to react rapidly to severe food shortage by lowering their metabolic rate to a basal level.
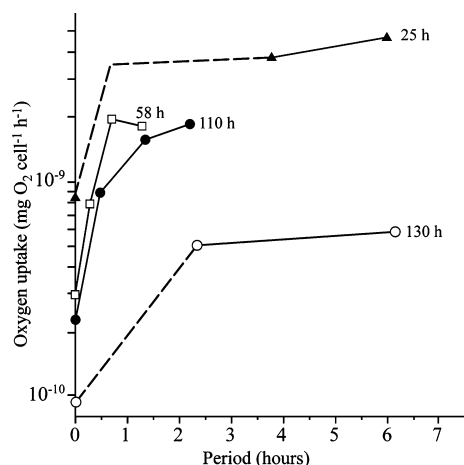
Fig. 5. Respiration rate of *Ochromonas* sp., starved for different periods of time, after the addition of bacterial cells at 2×10^8 ml^{-1} (modified from Fenchel 1982a).

The functional feeding response of marine ciliates has been evaluated for a number of isolates in culture (reviewed in Gismervik 2005). For six species of small non-loricate ciliates isolated from Norwegian coastal waters, Gismervik (2005) reported that feeding thresholds, below which no net ciliate growth occurred, were in the range of 600–3300 algal cells ml^{-1}, or 6–34 μg C l^{-1}. One of the species studied, *Strobilidium spiralis*, was observed to reduce its feeding effort below 20 μg C l^{-1}, resulting in cell shrinkage and death. Live observations of *S. spiralis* showed that the ciliates seemed inactive at low food concentrations (Gismervik 2005). In another case, survival (Morita 1997) of the dinoflagellate *Protoperidinium depressum* for up to 71 days at less than 1 μg C l^{-1} of diatoms could be ascribed to a reduction of the dinoflagellate's metabolic rate (Menden-Deuer *et al.* 2005).

There is, to date, little information regarding response of phagotrophic protists to low food abundance in the field. Lessard & Murrell (1998) did find sharply reduced grazing efforts by *in situ* phagotrophic protists once ultra-low food levels were reached. Using environmental assemblages of phyto- and protozooplankton from the Sargasso Sea, these authors reported a decrease in protist clearance rates below 0.1 μg chlorophyll *a* (Chl *a*) l^{-1}, and a near zero grazing rate at 0.04 μg Chl *a* l^{-1} (Fig. 6). Assuming carbon:chlorophyll ratios for small sized, open ocean phytoplankton in the range of 60–90 μgC μg chl *a* l^{-1}, a value of 0.1 μg Chl *a* l^{-1} would represent about 6–9 μg C l^{-1}, at the low end of ciliate feeding thresholds observed in culture (Gismervik 2005). A Chl *a* concentration of 0.04 μg l^{-1} is at the annual minimum found for the Sargasso Sea (Lessard & Murrell 1998), and also the minimum value reported for the North Pacific Central Gyre (Eppley *et al.* 1973), as well as for the Eastern North Atlantic Subtropical Gyre (Teira *et al.* 2005) (Table 1). Such similar minimum chlorophyll concentrations would be 'consistent with the idea that grazer behavior may determine the minimum level of phytoplankton biomass' (Lessard & Murrell 1998). However, we ought to keep in mind that near zero grazing on chlorophyll-containing particles does not necessarily mean that protists are not feeding. Alternative food sources include heterotrophic bacteria and other phagotrophic protists (*e.g.* Verity 1991b; Calbet *et al.* 2001; Juhl & Murrell 2005).

In the ocean, food particles are never completely exhausted, which implies that full starvation should never occur for protists or copepods. As with *Eucalanus hyalinus* females, phagotrophic protists in many parts of the ocean may be able to respond within a short time span – minutes to hours – with increased feeding activity in response to increased food abundance. For example, Saito *et al.* (2006) reported that heterotrophic *Gyrodinium* sp. increased dramatically in abundance over a period of days during an iron-enriched diatom bloom (>15 μg Chl *a* l^{-1}) in the Subarctic Northwest Pacific Ocean.

Patchiness and Top–down Control of Grazers

Abundances of potential food organisms vary over their vertical and horizontal distributions as a result of the balance between growth and mortality. Patchiness of various planktonic microbes occurs over a range of temporal and spatial scales, from seasonal phytoplankton blooms over

Fig. 6. Community clearance and ingestion rates of a natural grazer assemblage in the Sargasso Sea *vs.* chlorophyll concentration (modified from Lessard & Murrell 1998).
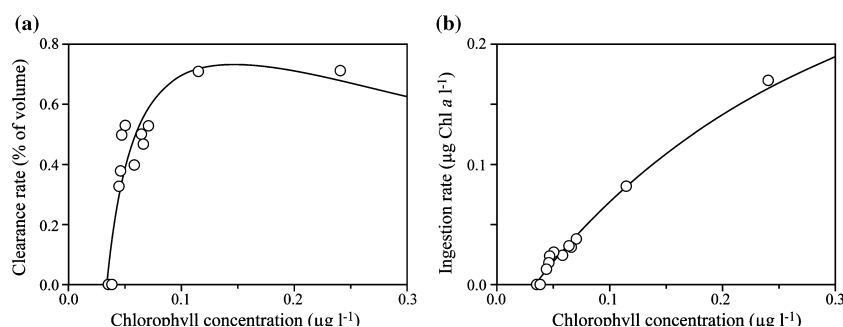
many square kilometers lasting days to weeks (Mann & Lazier 1996; Martin *et al.* 2002), to aggregations of prokaryotic and eukaryotic microorganisms within a few hundred cubic microns around individual detrital particles or other microsources of nutrients lasting minutes (Mitchell & Fuhrman 1989; Duarte & Vaqué 1992; Blackburn *et al.* 1998; Seymour *et al.* 2000).

Although mesoscale to microscale patchiness of phytoplankton, bacteria and heterotrophic protists have been widely hypothesized (*e.g.* Azam & Long 2001), actual observations of microbial aggregations in the ocean are relatively rare. Sampling volumes from 0.25 to 5000 ml in neritic waters of the northwestern Mediterranean Sea, Duarte & Vaqué (1992) observed pronounced patchiness at the milliliter scale, *i.e.* 10^7 bacteria ml^{-1} in surrounding waters of 10^5 bacteria ml^{-1}. They concluded 'that the processes regulating bacterial abundance operate at the centimeter scale.' Seymour *et al.* (2000) quantified distributions of bacteria on the millimeter scale in coastal regions of Australia. They found differences in bacterial abundance by a factor of 16 over a distance of 32 mm. As bacterial concentrations can vary by one order of magnitude over distances of 1–3 cm, the time for bacterivores (heterotrophic nanoflagellates) to encounter sufficient food in the epipelagic open ocean should not extend to hours but probably to <1 h.

Mesoscale to microscale aggregations of phytoplankton have also been observed in the sea. Thin layers of high phytoplankton abundance have been studied in several coastal ecosystems (Derenbach *et al.* 1979; Cowles *et al.* 1993; Dekshenieks *et al.* 2001; Rines *et al.* 2002; McManus *et al.* 2003). In these layers, which are a centimeter to meter thick and can extend to as much as a kilometer, phytoplankton biomass can be an order of magnitude greater compared with outside the layer, which should attract herbivorous protists and copepods (McManus *et al.* 2003).

Phagotrophic protists exhibit both chemoattraction to food and also change in swimming behavior depending on local prey abundance. Blackburn & Fenchel (1999) and Fenchel & Blackburn (1999) showed that bacterivorous protists can find food by chemical clues over distances of a few millimeters to a centimeter. Fenchel (1982b) observed that when bacterivorous flagellates were starved, they began to swim rapidly compared with slow swimming during feeding. As a swimming flagellate is thought to use only about 0.1% of its energy for motility (Fenchel 1982b), it would be bioenergetically inexpensive for starving flagellates to increase their swimming speed. Protists in general are thought to use a small fraction of their total energy budget for locomotion (Fenchel 1982b).

Herbivorous ciliates and dinoflagellates also exhibit chemotaxis, and have been observed to change their swimming behavior in response to the presence of prey. Verity (1988, 1991c) investigated chemosensory responses of isolates and of natural assemblages of herbivorous ciliates to monospecific cultures of potential algal prey. He found that the ciliates strongly preferred certain phytoplankton, and showed least chemosensory response to, or even avoidance of, the brown tide raphidophyte alga *Olisthodiscus* and a cyanobacterium, *Synechococcus.* Fenchel & Jonsson (1988) described differential swimming behavior for an aloricate pelagic ciliate, *Strombidium sulcatum*, in which starved cells swam in elongated helices with occasional tumbles (changes of direction), while feeding cells swam in tight circles. These swimming patterns would aid first in the search for food, and then to keep the ciliate within a patch of food. Menden-Deuer & Grünbaum (2006) found that the herbivorous marine dinoflagellate, *Oxyrrhis marina*, was able to modify its swimming behavior to stay within thin layers of phytoplankton created under laboratory conditions, resembling estuarine conditions.

How can organisms associated with the microbial food web remain at rather steady low abundances? The ability/potential, specifically of phagotrophs, to ingest large numbers of prey per unit time and grow as fast or faster than their prey implies that any localized aggregation of prey would be diminished rapidly, followed by a reduction in metabolic activity of the phagotrophs because of insufficient food ingestion for sustained growth. Rapid decrease in abundance of a prey population would imply that such an aggregation had developed without significant grazing pressure or other sources of mortality (*e.g.* viral infection), which again implies that rather few phagotrophs were present initially. It follows that phagotrophs (of a given size range) also occur in patches, *i.e.* are probably attracted chemically to prey aggregates (Verity 1988, 1991c, Price 1989; Fenchel & Blackburn 1999, Menden-Deuer & Grünbaum 2006). This leads to the hypothesis that the various motile components of the microbial food web are searching for food once prey abundance reaches a critically low concentration, and tend to aggregate where food is (temporarily) abundant. The aggregation of the smallest sized protists (bacterivorous nanoflagellates) around patches of picoplankton should then lead to an aggregation of larger protists which feed on the bacterivores (Verity 1991b; Jeong *et al.* 2007), which then may attract metazooplankton such as copepods. Such sequences could favor the development of (temporary) patches of different plankton components at different time intervals.

Is then patchiness of prey and predators essential for keeping the microbial food web components in the subtropical gyres at a low quasi steady-state? Patchiness of grazers is a function of the behavior, including perception

and rates of motion, feeding, growth and reproduction, of the various biotic components. Aggregations of various size classes of protist grazers in response to food patches may well facilitate top–down control of planktonic consumers, via local 'trophic cascades,' although this process has not yet been demonstrated for <200 μm grazers in the sea.

Mixotrophy and Prey Switching

In the ocean many species of protists are neither exclusively heterotrophic nor autotrophic, but rather mixotrophic (Stoecker 1998; Caron 2000; Jones 2000). This implies that certain autotrophs can obtain energy by ingesting other protists, while certain heterotrophs can rely on chloroplasts to obtain energy when food is scarce. However, being a mixotroph could carry extra energetic costs involved with maintaining cellular machinery for both photosynthesis and phagotrophy (Raven 1997). Mixotrophs are thought to have lower maximum growth rates compared with either obligatory phagotrophs or phototrophs of similar size (Stoecker 1998). The fact that phagotrophy is common among phytoflagellates (Stoecker 1998; Caron 2000) suggests that there is survival value to this mixed trophic mode. Phytoflagellates can gain both organic carbon for energy, and macro- and micronutrients for biosynthesis, by consuming other cells (Caron 2000). Phagotrophic ciliates which retain chloroplasts from ingested algal prey can gain considerable extra carbon. For example photosynthesis by captured chloroplasts has been estimated to yield about a third of the daily organic carbon requirement for the common mixotrophic ciliate *Laboea strobila* (Stoecker *et al.* 1988). In essence, numerous protists including ciliates and dinoflagellates are mixotrophs, which enhance the probability of survival in a nutritionally dilute environment (Conover 1968).

To date, there is very little in the literature on the capacity of phagotrophic protists to switch between alternative prey types, although all groups of protists are known to choose among available prey. Prey selectivity by bacterivorous flagellates has been found in several studies (Jürgens & DeMott 1995; Strom 2000). Marine ciliates preferentially graze one species of phytoplankton prey over another (Stoecker *et al.* 1988; Verity 1988, 1991c). Tintinnids have been shown to prefer dinoflagellates to other algae, live algae to plastic microspheres, and microspheres to dead algae (Stoecker *et al.* 1988). The ingestion of a prey organism by a ciliate can vary because of sequential steps such as encounter, capture and handling, aside from any active selection or use of chemical cues (Verity 1991a). Dinoflagellates, which tend to be raptorial feeders rather than filter feeders, are also likely to show selective feeding. Buskey (1997) investigated the feeding behavior of an armored dinoflagellate, *Protoperidinium pellucidum*, which captures and digests prey extracellularly via a feeding veil. He found that *P. pellucidum* fed preferentially on diatoms over dinoflagellate prey, and also selected between diatom species. Size of prey did not appear to matter to the dinoflagellate. More recently, Martel (2006) found that chemosensory response and prey ingestion in the heterotrophic dinoflagellate *Oxyrrhis marina* did not appear to be closely coupled, and suggested that the biochemical mechanisms of chemosensory behavior and of prey capture may differ.

Processes Resulting in Quasi Steady-State Abundances

The central question we wish to address is: 'Which variables can influence feeding performances of herbivorous and omnivorous grazers in the ocean?' As food abundances decrease, clearance rates of flagellates (Capriulo 1990, and references therein), of ciliates (Jonsson 1986; Kivi & Setälä 1995; Gismervik 2005), of phagotrophic dinoflagellates (Kim & Jeong 2004) and of calanoid copepods (Corner *et al.* 1972; Paffenhöfer 1988) increase. For copepods, as shown earlier, those clearance rates increase towards a low food level below which they decrease quite sharply (Figs 1 and 2). This is similar to the above mentioned result of Lessard & Murrell (1998, Fig. 6). Which are the processes that actually lead to these respective increases, and eventual decreases of clearance rates, which *in situ* should lead to quasi steady-state abundances of chlorophyll, prokaryotes, eukaryotes, copepods, and, most likely, various protist groups in the oligotrophic open ocean?

As food concentrations decrease, the distance at which the calanoid *Eucalanus pileatus* perceives neighboring diatom cells increases up to a maximum distance, which then does not increase with further diminishing diatom abundance (Paffenhöfer and Lewis 1990, Fig. 7). This implies that *E. pileatus* increases the volume of water cleared of food cells as food concentrations decrease due to increasing sensory performance. While at 0.1 mm^3 of *Thalassiosira weissflogii*, *E. pileatus* ingested 32% of its body carbon per day, at 0.03 mm^3 l^{-1} it obtained only 10%. The copepod had reached the maximum of its sensory performance at 0.1 mm^3 l^{-1}, *i.e.* was unable to improve on it as the food concentration was lowered. As this copepod respires *c.* 15% of its body mass per day it will not obtain sufficient food to support itself at the food concentration of 0.03 mm^3 l^{-1}. At this rate *E. pileatus* has to decide what to do. *Eucalanus hyalinus, C. helgolandicus*, and other copepods, and the herbivorous microzooplankton in the study of Lessard & Murrell (1998) do not suddenly stop their feeding activity at such
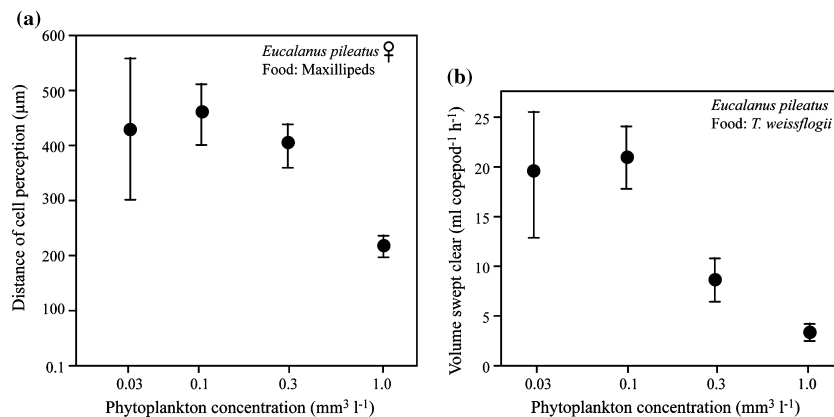
(a)

(b)

Fig. 7. Distance of cell perception and clearance rate of the calanoid *Eucalanus pileatus* in relation to the concentration of the diatom *Thalassiosira weissflogii* (modified from Paffenhöfer & Lewis 1990).

insufficient food levels, but rather decrease it to the level of just supporting their metabolic needs.

As they most likely are moving, grazers could detect a nearby patch of abundant food particles. This would be similar to the results of Price (1989) when the euphausiid *Thysanoessa raschii* was observed at finding a patch of algae. At the very low levels of food particles in the oligotrophic ocean, heterotrophic protists, perceiving food particles at their maximum sensitivity, should easily find suitable patches of food (at the 1 cm or ml scale, Duarte and Vaqué 1992) and remain in it until the food abundance has reached a level which would not support their regular metabolic needs anymore. At this time the protists would start searching again, and would temporarily reduce their metabolism while physical mixing processes at the cm-scale and higher would enhance encounters with water masses of higher prey abundance. Such patchiness of protists would permit intermittent growth of food organisms in those bodies of water devoid of these feeders. The probability of occurrence of patches of various types of protists in the ocean is supported by the findings of various authors (*e.g.* Seymour *et al.* 2000, and references therein). There is no information about the occurrence of patches of phytoplankton on the cm-scale in the open ocean. The effects of diel warming and cooling in the upper mixed layer of subtropical gyres, and the effects of turbulence/mixing in the thermocline should affect the sizes of patches of the various protist taxa.

Conclusions

Our survey of prior studies suggests that several biological mechanisms may contribute to quasi-steady state concentrations of various size and phylogenetic groups of plankton in the open ocean. All heterotrophic plankton, including bacteria, protists, and copepods, appear to be able to reduce their metabolic rate when food abundance

is low. Motile consumers: flagellated bacteria, protists, and copepods, have also been shown to respond to patches of food, resulting in aggregations of consumers around or within food patches. Such aggregation may facilitate a 'trophic cascade' of top–down control of grazers, although there is as yet no direct evidence for this. Finally, mixotrophy is widespread among phagotrophic protists, and probably contributes to their ability to survive at low prey abundance.

Efforts Towards an Understanding of Governing Mechanisms

We have hypothesized that taxon-specific behavior governs the quasi steady-state of various organismic groups in oligotrophic open ocean ecosystems, actually a quasi steady-state of the microbial food web. How can this hypothesis be tested experimentally? Suggestions to address the observation of quasi steady-state of food organisms were made by Strom *et al.* (2000). Other suggestions include those by Landry (2002, p. 33) on experimentation and hypothesis testing. As phagotrophic protists are the main grazers of both bacteria and of phytoplankton in the open ocean, and are more amenable to laboratory culture and experimentation compared with open ocean copepods, we propose a set of experiments based on examining the behavior and growth/survival of a variety of phagotrophic protists at low food concentrations.

1 A first step could be similar to the suggestion by Strom *et al.* (2000): Observe over time, under controlled conditions, several different and representative taxa of the heterotrophic nanoplankton and microplankton from an open ocean system, feeding on one or two food taxa while reducing the food abundance slowly, *i.e.* simulating *in situ* conditions. Both the cell-specific rate of feeding, and the motion behavior of the protistan grazers, would be quantified.

2 Observe changes in the motion behavior of the micrograzers (including bacterivorous flagellates, and herbivorous ciliates and dinoflagellates), at decreasing ultralow food levels, and also when adding modest increments of food. This could result in either reductions in activity for the grazers or in increases in activity for the prey, similar to the idea of Fenchel (1982a,b) but for environmentally relevant concentrations of grazers and prey.

3 Test for changes in physiological states of protists under different nutritional conditions, for example using molecular probe assay kits, which evaluate various aspects of the health of eukaryotic cells with different fluorochrome-tagged compounds and combinations of flow cytometry and microscopy.

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