



## Significance of predation by protists in aquatic microbial food webs

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### Abstract

Predation in aquatic microbial food webs is dominated by phagotrophic protists, yet these microorganisms are still understudied compared to bacteria and phytoplankton. In pelagic ecosystems, predaceous protists are ubiquitous, range in size from 2  $\mu\text{m}$  flagellates to  $>100 \mu\text{m}$  ciliates and dinoflagellates, and exhibit a wide array of feeding strategies. Their trophic states run the gamut from strictly phagotrophic, to mixotrophic: partly autotrophic and partly phagotrophic, to primarily autotrophic but capable of phagotrophy. Protists are a major source of mortality for both heterotrophic and autotrophic bacteria. They compete with herbivorous meso- and macro-zooplankton for all size classes of phytoplankton. Protist grazing may affect the rate of organic sinking flux from the euphotic zone. Protist excretions are an important source of remineralized nutrients, and of colloidal and dissolved trace metals such as iron, in aquatic systems. Work on predation by protists is being facilitated by methodological advances, e.g., molecular genetic analysis of protistan diversity and application of flow cytometry to study population growth and feeding rates. Examples of new research areas are studies of impact of protistan predation on the community structure of prey assemblages and of chemical communication between predator and prey in microbial food webs.

### Introduction

Over the past 30 years it has become increasingly obvious that phagotrophic protists play important ecological roles in aquatic food webs. This is borne out by the diversity of research topics involving these microorganisms, which cover the full gamut of ecological perspectives, from cellular, population, and community, up to the level of whole ecosystems. In this review we will emphasize the ecosystem-level significance of phagotrophic protists, particularly in marine microbial food webs. We will also mention some recent work on the interactions between populations and between individual organisms (for a more thorough discussion of these kinds of interactions see Weisse (this volume)). We will end with a brief overview of future research directions, including an exciting new research area dealing with how cell-to-cell communication may affect the outcome of predator–prey interactions within pelagic microbial food webs.

### Phagotrophic protists

Phagotrophy is an ancient mode of nutrition for protists, predating photosynthesis (Dyer & Obar 1994; Vickerman 1998). It is thus not surprising that phagotrophy is widespread among the major phylogenetic branches of the protistan family tree (Figure 1). Of these major groups, only diatoms have no known species capable of ingesting particles. A newly described class of marine phytoflagellates, the Bolidophyceae, which is most closely related to the diatoms (Guillou et al. 1999a), has not yet been tested for phagotrophy. Some groups of protists, notably the amoeboid protists, bodonids (kinetoplastids), choanoflagellates, and ciliates, are strictly, or mainly, phagotrophic. The remaining protist groups include species that are either phototrophic or phagotrophic, or both. In the case of the chlorophytes, all known species are phototrophic, but one species of prasinophyte, *Micromonas pusilla*, has been observed ingesting bacteria (Gonzalez et

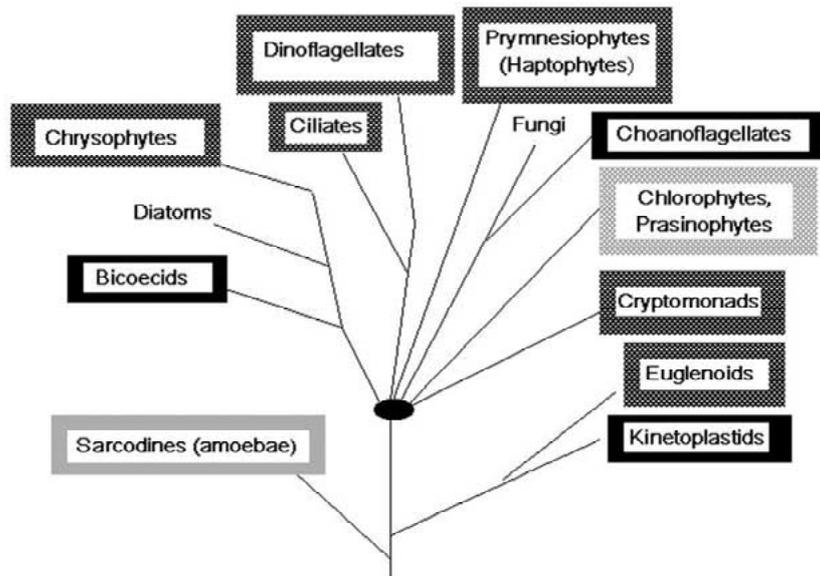


Figure 1. Distribution of phagotrophy among broad taxonomic groups of free-living protists in aquatic ecosystems. The diagram shows general phylogenetic relationships among eukaryotic microbes based on gene sequence comparisons of small subunit rRNA, from Figure 1 of Sherr & Sherr (2000). Genetic distances are not drawn to absolute scale. Phagotrophic (ability to ingest particles) has been demonstrated for heterotrophic and/or autotrophic species in all the groups except for diatoms and fungi. Groups with black-bordered boxes are strictly phagotrophic; groups with dark checkered boxes include strictly autotrophic, strictly phagotrophic, and mixotrophic species; the chlorophyte/prasinophyte group, so far as is presently known, includes only autotrophic species, but one prasinophyte, *Micromonas pusilla*, has been found to ingest bacteria.

al. 1993b). Mixotrophy, in which cells gain energy and nutrients both by photosynthesis and by ingesting prey, is common among protists (Arenovski et al. 1995; Havskum & Hansen 1997; Caron 2000).

Protists are important in the functioning of aquatic ecosystems because they are ubiquitous and abundant in all types of habitats. Phagotrophic protists, including heterotrophic and mixotrophic flagellates, ciliates and dinoflagellates, are literally found from pole to pole, from lakes in the dry valleys of Antarctica (Laybourn-Parry et al. 2000) to seawater under the Arctic ice cap (Sherr et al. 1997). Phagotrophic protists are important components of food webs in extreme habitats such as sea ice (Palmisano & Garrison 1993; Archer et al. 1996a; Buck et al. 1998; Scott et al. 2001), solar salterns with salinities as high as 150‰ (Pedros-Alio et al. 2000), and the deep ocean (Gooday & Lamshead 1989; Turley & Carstens 1991; Buck et al. 2000). Protists are similar in size to their microbial prey: bacteria, algae, and other heterotrophic protists; their growth potential is as great as that of their microbial prey; and their high rate of metabolism facilitates carbon and energy flux through ecosystems (Fenchel 1987; Sherr & Sherr 1994; Finlay 2001). In pelagic ecosystems,

the community of phagotrophic protists typically is dominated by heterotrophic flagellates, ciliates, and dinoflagellates (Capriulo 1990; Sherr & Sherr 1994); however naked amoebae occur sporadically (Capriulo 1990; Vors 1992a; Murzov & Caron 1996), and pelagic sarcodines are present at low biomass in the open ocean (Capriulo 1990; Swanberg & Caron 1991).

### Significance of protistan phagotrophy at the ecosystem level

By far, the greatest amount of attention given to the role of phagotrophic protists in aquatic ecosystems has been focused on the quantitative role of protists as consumers of other microbial cells. It is by now well established that (1) protistan predation can be a significant source of mortality for suspended bacteria in both freshwater and marine ecosystems, (2) protists are important grazers of phytoplankton in marine systems, (3) protists can and do consume other heterotrophic protists (and sometimes prey on metazoan eggs and small crustaceans), (4) heterotrophic protists can be a significant food source for metazooplankton, and (5) excretion of nitrogen and phosphorus compounds,

and also of trace metals such as iron, by phagotrophic protists is a major source of regenerated nutrients in aquatic systems.

### Protistan bacterivory

From the seminal papers by Pomeroy (1974) and Azam et al. (1983) to the present, intensive research has been carried out on protistan bacterivory in both freshwater and marine systems (Pace et al. 1990; Sanders et al. 1992; Simon et al. 1998; Simek et al. 1999; Cristaki et al. 1999; Strom 2000; Weisse this volume). Much of the focus of this research has been on heterotrophic (non-plastid containing) flagellates. The primary bacterivores in aquatic ecosystems are typically small heterotrophic flagellates, generally cells  $<5 \mu\text{m}$  in size (Sherr & Sherr 1989, 1991a; Strom 2000). However, bacterivory by autotrophic flagellates is common in freshwater systems and is increasingly reported in marine systems (Nygaard & Tobiesen 1993; Caron 2000). In eutrophic freshwater and coastal marine systems, ciliates can also be significant grazers of bacteria (Sherr et al. 1989, 1991a; Weisse & Muller 1998; Simek et al. 1999).

There is an extensive literature on protistan bacterivory in both marine and freshwater ecosystems. Reviews on this topic include those of Sieburth (1981), Fenchel (1984, 1986), Pace (1988), Gude (1989), Sherr & Sherr (1994), Vaque et al. (1994), Strom (2000), Sherr & Sherr (2002), and Weisse (this volume). A variety of methodologies have been used to evaluate the rate of protistan bacterivory in natural pelagic systems, including uptake or disappearance of labeled surrogate prey cells, digestive enzyme activity of bacterivorous protists, manipulation experiments including size fraction and dilution, and uptake of radiolabeled prey (Zubkov et al. 1998; Sleigh & Zubkov 1998; Strom 2000; Sherr & Sherr 2002). These assays were designed to yield quantitative rates of carbon flow from bacteria to bacterivorous protists, which could be used in construction of dynamic food web models. A small number of studies have also evaluated bacterivory in benthic systems (e.g., Kemp 1988; Honedeveld et al. 1992; Epstein 1997). The result of the pelagic studies has been to confirm the importance of protists as a routine and significant source of mortality for suspended bacteria in most aquatic systems studied.

Protistan bacterivory is complicated by the fact that the prokaryotic community in aquatic ecosystems in-

cludes autotrophic as well as heterotrophic bacteria in the picoplankton (0.2–2  $\mu\text{m}$ ) size class. This is particularly important in the sea, where photosynthetic prokaryotes are abundant: *Synechococcus*, 1–1.5  $\mu\text{m}$ -sized cells with phycobiliprotein accessory pigments; and the prochlorophyte, *Prochlorococcus*,  $\sim 0.8 \mu\text{m}$  in size with divinyl chlorophyll *a* and *b* and carotenoid accessory pigments. In addition, it has been proposed that other marine bacteria are phototrophic via non-oxygenic photosynthetic pathways, i.e., can use light energy to generate ATP (Beja et al. 2000, 2001; Kolber et al. 2000). The two major groups of autotrophic bacteria are differently distributed in the sea: *Synechococcus* cells occur at concentrations of  $10^3$  to  $10^5 \text{ ml}^{-1}$ , and are most abundant in coastal and continental shelf waters, while *Prochlorococcus* abundance is on the order of  $10^5 \text{ cells ml}^{-1}$ , and is highest in oligotrophic ocean gyres (Li 1998; Partensky et al. 1999; Zubkov et al. 2000). Prochlorophytes can make up a large fraction of total bacterial cells in the euphotic zone of the open ocean (Campbell et al. 1994). *Prochlorococcus* cannot easily be distinguished from heterotrophic bacteria using standard epifluorescence microscopy enumeration techniques; detection of prochlorophytes living at shallow water depths is problematic even with flow cytometry due to the low cell-specific pigment fluorescence caused by photobleaching (Zubkov et al. 2000). With respect to ecosystem function, protistan ‘bacterivory’ in ocean regions where *Synechococcus* or *Prochlorococcus* is abundant is in fact ‘herbivory’ as well.

### Herbivory

While the ecosystem-level importance of protistan bacterivory is widely accepted and studied, the role of protists as herbivores remains under-appreciated. We can not state strongly enough that in the euphotic zone of the world ocean, the ecosystem-level impact of protistan herbivory is more significant than that of protistan bacterivory. This may be true also for some freshwater systems such as large oligotrophic lakes, but there is less information on the impact of protists as herbivores in freshwater. In the marine pelagic, protists are ideal herbivores because protists are able, using various feeding strategies, to consume all sizes of autotrophic cells, from bacterial-sized *Prochlorococcus* and *Synechococcus* to large dinoflagellates and chain-forming diatoms (Smetacek 1981; Hall et al. 1993; Jacobson & Anderson 1996; Jeong 1999a,b;

Table 1. Comparison of abundance (cells ml<sup>-1</sup>), biomass ( $\mu\text{g C l}^{-1}$ ), and average cell size (equivalent spherical diameter, ESD), of ciliates and heterotrophic dinoflagellates, and heterotrophic dinoflagellate biomass as percent of heterotrophic protist biomass in Oregon coastal waters in January 2001. Data is based on 45 discrete water samples; average value  $\pm$  one standard deviation

	Abundance (cells ml <sup>-1</sup> )	Biomass ( $\mu\text{g C l}^{-1}$ )	Cell size (ESD, $\mu\text{m}$ )	% of total biomass
Ciliates	1.3 $\pm$ 0.5	0.82 $\pm$ 0.45	21 $\pm$ 3	52 $\pm$ 17
Heterotrophic dinoflagellates	10 $\pm$ 5	0.77 $\pm$ 0.42	11 $\pm$ 4	48 $\pm$ 17

Sanders et al. 2000). In addition, protists can grow as fast, or faster, than phytoplankton cells, and thus can keep up with phytoplankton blooms (Sherr & Sherr 1992, 1994). We also stress the point that heterotrophic dinoflagellates are also major grazers of phytoplankton and can be equal to ciliates in terms of planktonic biomass (Hansen 1991; Strom 1991; Neuer & Cowles 1994; Sherr & Sherr 1994; Strom & Strom 1996; Archer et al. 1996b). As an example, Table 1 shows typical results from a recent data set in an ongoing project to quantify microzooplankton stocks in the upper water column off the Oregon coast. Abundance and biomass of ciliates were determined by fixation with acid Lugol's solution, settling and inverted microscopy, and of heterotrophic dinoflagellates by fixation with formalin, filtration, and epifluorescence microscopy (Sherr et al. 1993). Heterotrophic dinoflagellates comprised, on average, 48% of the combined ciliate plus dinoflagellate biomass in this sample set (Table 1).

A consideration of the biomass availability of various prey categories for phagotrophic protists illustrates why protistan herbivory should be of greater magnitude compared to consumption of heterotrophic bacteria in the sea. Two general scenarios for amounts of prokaryotic and eukaryotic prey biomass are presented in Table 2, based on literature values for typical cell abundances and for cell-specific carbon contents in oligotrophic and mesotrophic marine pelagic ecosystems (Fukuda et al. 1998; Li 1998; Zubkov et al. 2000; Blanchot et al. 2001). In the open ocean scenario, *Prochlorococcus* makes up almost half of the total prey biomass. Combining *Prochlorococcus*, *Synechococcus* and eukaryotic phytoplankton, autotrophic cells comprise 70% of the total prey biomass available to phagotrophic protists. In the coastal water scenario, eukaryotic phytoplankton comprise 57%, heterotrophic bacteria 32%, and *Synechococcus* 11%

of total biomass. Autotrophic microbes make up 68% of a biomass of 94  $\mu\text{g C l}^{-1}$ ; the chlorophyll concentration, 1–2  $\mu\text{g l}^{-1}$ , would be an order of magnitude higher than in the open ocean scenario. Note that in both of these cases, about 70% of prey biomass is autotrophic, and only 30% is heterotrophic bacteria.

This exercise highlights the fact that, in most regions of the sea, the bulk of the food resources available to protists is composed of autotrophic cells. The biomass of heterotrophic bacteria is typically on the order of 5 to 20  $\mu\text{g C l}^{-1}$  in open ocean systems, a fraction of the total microbial biomass available as food to protists (Ducklow 2000). In addition, phytoplankton production rates are generally higher compared to bacterial production rates in aquatic ecosystems (Cole et al. 1983, Ducklow 2000). It is not surprising that protists, from the smallest flagellates to large ciliates and dinoflagellates, have evolved strategies for consuming phytoplankton.

One could also consider the effort required by individual protists to obtain sufficient prey carbon to support one cell doubling per day at carbon-based prey concentrations that obtain in most marine systems. The average clearance rates required for a 2- $\mu\text{m}$  flagellate, a 5- $\mu\text{m}$  flagellate, a 20- $\mu\text{m}$  dinoflagellate, and a 40- $\mu\text{m}$  ciliate to obtain triple the amount of cell carbon (33% growth efficiency) in 24 h of feeding, at three carbon-based prey concentrations, are presented in Table 3. Two points can be made here. First, only the smallest flagellates should be able to survive and grow at very low clearance rates (1–5 nl cell<sup>-1</sup> h<sup>-1</sup>). [It should be noted that marine flagellates capable of ingesting material even smaller than bacteria, including viruses (Gonzalez & Suttle 1993) and high molecular weight dissolved organic polysaccharides and proteins (Tranvik et al. 1993) would have an alternate source of nutrition.] A 5- $\mu\text{m}$  cell would be required to clear prey at a rate of 20–70 nl

Table 2. Hypothetical proportional distribution of prey biomass (autotrophic microbes and heterotrophic bacteria) available for consumption by phagotrophic protists, based on literature data, in: (A) the euphotic zone of an open ocean gyre, and (B) of a coastal ocean system. In both cases, the majority of available biomass is present in autotrophic cells

Region	Prey	Abundance (10 <sup>5</sup> cells ml <sup>-1</sup> )	fg C cell <sup>-1</sup>	Biomass (μg C l <sup>-1</sup> )	% of total
Open ocean gyre Chl- <i>a</i> ~0.1 μg l <sup>-1</sup>	Heterotrophic bacteria	4	12 <sup>1</sup>	4.8	30
	<i>Prochlorococcus</i>	2	40 <sup>2</sup>	8	49
	<i>Synechococcus</i>	0.02	200 <sup>2</sup>	0.4	2.5
	Eukaryotic phytoplankton	0.02	1500 <sup>2</sup>	3	18.5
	Total:			16.2	
Coastal waters Chl- <i>a</i> ~1–2 μg l <sup>-1</sup>	Heterotrophic bacteria	10	30 <sup>1</sup>	30	32
	<i>Prochlorococcus</i>	0	40 <sup>2</sup>	0	0
	<i>Synechococcus</i>	0.5	200 <sup>2</sup>	10	11
	Eukaryotic phytoplankton	0.2	3000 <sup>2</sup>	60	57
	Total:			94	

<sup>1</sup>Fukuda et al. (1998).

<sup>2</sup>Li (1998), Zubkov et al. (2000), Blanchot et al. (2001).

cell<sup>-1</sup> h<sup>-1</sup> to sustain a reasonable growth rate. Larger protists should, in theory, have to clear at higher rates, hundreds of nl to several μl cell<sup>-1</sup> h<sup>-1</sup> to obtain reasonable amounts of food for growth. Studies of grazing rates of various groups and size classes of protists in natural habitats have, in fact, yielded estimates of clearance rates in the general ranges of those suggested in Table 3 (e.g., Sherr et al. 1991b; Simek & Strassburgova 1992; Jurgens et al. 1996; Hwang & Heath 1997; Sherr et al. 1997; Jeong 1999; Weisse this volume).

Secondly, all sizes of phagotrophic protists would benefit, in terms of lower required clearance rates, from omnivorous feeding across prey categories to increase the available biomass of prey. Heterotrophic nanoflagellates in the size category of 5–20 μm may be primarily herbivorous (Sherr & Sherr 1991, 1992; Sherr et al. 1991b). Phytoplankton-consuming flagellates less than 20 μm in size include small gymnodinoid dinoflagellates (Strom 1991; Sherr et al. 1992) and the cryptomonad-like *Leucocryptos marina* (Vors 1992b). Even <5-μm nanoflagellates cannot be assumed to be strictly bacterivorous. For example, we have observed abundant 2–5-μm sized heterotrophic flagellates in the central Arctic Ocean (Sherr et al. 1997) and in the Oregon upwelling system (Sherr unpublished data) that ingested 1.5–2-μm diameter algal cells and coccoid cyanobacteria as well as het-

erotrophic bacteria. Mixotrophic nanoflagellates, e.g., species of *Chrysochromulina*, have been observed to ingest pico-algal cells such as 2.3-μm *Micromonas pusilla* (Jones et al. 1993; Hansen 1998). For larger protists too, omnivory, i.e., feeding across a range of prey types and sizes, is a common theme (e.g., Hansen 1998; Jeong 1999).

Sakka et al. (2000) demonstrated by direct measurements that protistan herbivory was greater in magnitude compared to protistan bacterivory in an oligotrophic atoll lagoon. In the lagoon, phytoplankton biomass was dominated by coccoid cyanobacteria and <3-μm algae. Grazing rate assays showed that the major pathway of carbon flow was from phytoplankton to smaller-sized phagotrophic protists. Protist consumption of heterotrophic bacteria contributed relatively little to fluxes in this food web (Sakka et al. 2000).

#### Documentation of the magnitude of protistan herbivory in the sea

Field research has comprehensively documented the quantitative significance of protistan herbivory in the world ocean during the 1990s. A large part of this effort was due to the Joint Global Ocean Flux Study (JGOFS) and allied programs, international efforts designed to examine broad patterns and controls of carbon cycling within large geographical regions of

Table 3. Average clearance rates required for various sized protists (size is given as equivalent spherical diameter in microns) to obtain sufficient prey carbon to support one cell doubling per day, assuming a gross growth efficiency of 30% (Zubkov & Sleigh 1997; Straile 1997). Carbon contents of protists were estimated based on cell biovolume using the equation of Lessard & Murrell (2000) for non-diatom protists. Clearance rates ( $\mu\text{l cell}^{-1} \text{h}^{-1}$ ) at three difference prey concentrations ( $\mu\text{g C l}^{-1}$ ) are given

Protist size ESD ( $\mu\text{m}$ )	Clearance ( $\mu\text{l h}^{-1}$ )		
	Low prey biomass ( $10 \mu\text{g C l}^{-1}$ )	Medium prey biomass ( $30 \mu\text{g C l}^{-1}$ )	High prey biomass ( $60 \mu\text{g C l}^{-1}$ )
2	0.009	0.003	0.001
5	0.12	0.04	0.02
10	0.8	0.3	0.1
20	2.6	0.9	0.4
40	20	7	3.5

the world ocean (e.g., Boyd & Harrison 1999; Burkill 1999; Koeve & Ducklow 2001; Murray 1995 & 1996). In addition, many smaller-scale research programs designed to evaluate the structure of planktonic food webs were carried out in other regions of the world ocean during this period. Multiple expeditions were launched in the Northeast Atlantic, the Equatorial Pacific, the Indian and the Southern Oceans as well as in the subarctic Pacific. One component of these studies was assessment of the role of phagotrophic protists in carbon and energy flow, i.e., their role as components of the euphotic zone food webs in these regions, and in particular, the role of protists as herbivores.

A valuable aspect of these expeditions was that a standard approach, the Landry-Hassett dilution assay (Landry 1993) was used to estimate microzooplankton herbivory, thus facilitating comparison of data across regions. Dolan et al. (2000) reviewed studies on microzooplankton grazing using the Landry-Hassett dilution approach during this decade, and showed that the annual number of dilution experiments increased about 10-fold during from 1992 to 1999. Table 4 summarizes results of these studies (not all inclusive) in terms of the percentage of daily primary production or phytoplankton standing stock biomass grazed per day by microzooplankton (mostly phagotrophic protists) in various regions of the world ocean. Despite the artefactual problems inherent in the dilution assay approach, these data do support the notion that protists rather than metazooplankton are routinely the major herbivores in marine waters. This finding has broad implications for our understanding of the fate of organic carbon in the ocean (Legendre & Le Fevre

1995; Legendre & Rassoulzadegan 1996; Thingstad et al. 1997; Calbet 2001).

### Role of phagotrophic protists in nutrient recycling

A consequence of protistan grazing is release of waste products into the environment: both undigested components of ingested prey as dissolved and particulate organic matter (Nagata & Kirchman 1990; Strom et al. 1997; Ferrier-Pages et al. 1998; Nagata 2000), and as dissolved inorganic nutrients, particularly ammonium and phosphate (Caron & Goldman 1990; Dolan 1997). Thus protistan grazing provides substrates for further growth of their prey, both heterotrophic bacteria (Sieburth & Davis 1982; Jumars et al. 1989) and autotrophic cells (Dolan 1997).

The capacity of many species of phytoflagellates to phagocytize gives these phytoplankters an advantage in the acquisition of nutrients in a chemically dilute environment. Mixotrophic algae ingest bacteria and eukaryotic prey to gain both organic substrates and inorganic nutrients (Arenovski et al. 1995; Caron 2000). In systems in which iron is a limiting micronutrient, consumption of iron-rich bacterial cells is an adaptive strategy for phagotrophic algae (Barbeau et al. 1996; Maranger et al. 1998). Bacterivorous flagellates may also experience iron limitation, and thus ingestion of prokaryotic prey with high iron concentrations can be important to heterotrophic as well as autotrophic protists (Chase & Price 1997). Mixotrophic phytoplankton have also been shown to be capable of directly ingesting colloidal iron particles for iron nutrition (Nodwell & Price 2000). Barbeau et al. (2001) demonstrated that

Table 4. Summary of estimates of grazing (likely not all-inclusive) by phagotrophic protists on phytoplankton in the world ocean, using the The Landry-Hassett dilution assay

Ocean region	% primary production grazed day <sup>-1</sup>	% phytoplankton stock grazed day <sup>-1</sup>	Reference
<i>Coastal waters:</i>			
Halifax Harbor	40–100	21–50	Gifford 1988
Rhode River Estuary	45–104	17–80	Gallegos 1989
Hiroshima Bay		12–75	Kamiyama 1994
Monterey Bay, California		22–55	Waterhouse & Welschmeyer 1995
Western Gulf of St. Lawrence	54–>100	33–42	Tamigneaux et al. 1997
San Francisco Bay	0–265		Murrell & Hollibaugh 1998
Estuary of Mundaka, Spain	54–94		Ruiz et al. 1998
Gironde Estuary, France	73–136	25–44	Sautour et al. 2000
Logy Bay, Newfoundland		16–131	Putland 2000
Norwegian fjords	20–100		Verity & Vernet 1992
	47–78		Archer et al. 2000
Oregon, USA coastal upwelling	0–120		Neuer & Cowles 1994
New Zealand coast	15–213		James & Hall 1998
Coastal North Pacific	0–185		Strom et al. 2001
<i>Northern Gulf of Mexico</i>			
	30–90		Strom & Strom 1996
	42–214		Fahnenstiel et al. 1995
<i>North Atlantic Ocean:</i>			
North Atlantic spring bloom	37–100		Verity et al. 1993
Northwestern Sargasso Sea	0–245		Lessard & Murrell 1998
Temperate and subtropical northeast Atlantic (summer)	63–300	8–41	Gaul et al. 1999
		23–77	Stelfox-Widdicombe et al. 2000
<i>Pacific Ocean:</i>			
NE Subarctic Pacific	74–100		Boyd et al. 1995
Equatorial Pacific	70–133		Verity et al. 1996
	59–83		Latasa et al. 1997
<i>Indian Ocean</i>			
Arabian Sea	38–78	67–131	Reckermann 1997
Western Arabian Sea	50–240		Landry et al. 1998
<i>Southern Ocean</i>			
Bellingshausen Sea (marginal ice zone)	21–271	3–40	Burkill et al. 1995
Atlantic sector	0–83	0–51	Froneman & Perissinotto 1996
Antarctic Circumpolar Current	10–30		Klaas C. 1997
Waters surrounding Prince Edward Islands	71	8	Froneman & Balarin 1998
Ross Sea	Negligible		Caron et al. 2000

heterotrophic marine flagellates can recycle thorium as well as iron from bacterial prey. However, these authors also found that the various species tested differed in their ability to remobilize trace metals from ingested prey. Landry et al. (2000) analysed the impact of

protist grazing during the second *in situ* iron fertilization experiment in the Equatorial Pacific (IronEx II). They found that protist grazers responded quickly to iron-stimulated phytoplankton growth, consumed all size classes of phytoplankton, and likely efficiently re-

cycled nutrients within the iron-enriched patch. These various studies suggest that uptake of prey cells and iron particles, followed by excretion of soluble iron, by phagotrophic protists, could be a significant part of the overall iron flux through pelagic food webs in iron-limited open ocean systems.

### Phagotrophic protists as food

An important ecosystem-level function of phagotrophic protists is to channel the production of microbes at the base of food webs (bacteria and phytoplankton) to higher trophic levels. There has been debate about the quantitative significance of trophic transfers involving protists (e.g., Ducklow et al. 1986; Sherr et al. 1987; Koshikawa et al. 1996), but there is no doubt that heterotrophic protists represent food for a variety of other consumers. The largest body of studies on this subject deals with ciliates and heterotrophic dinoflagellates as food for mesozooplankton (reviewed in Stoecker & Cappuzo 1990; Verity & Paffenhofer 1996; Perez et al. 1997; Jeong 1999). In regions of the ocean where most phytoplankton are  $<5 \mu\text{m}$  in size, protists may be a primary source of food for copepods and other zooplankters (Miller et al. 1991; Calbet & Landry 1999). Even in mesotrophic systems characterized by diatom blooms, phagotrophic protists can serve as an important trophic link between phytoplankton and mesozooplankton (Kleppel 1993; Fessenden & Cowles 1994). Heterotrophic dinoflagellates, which are rich in fatty acids and sterols, represent a high quality food for copepods (Klein Breteler et al. 1999). Planktonic phagotrophic protists can also serve as a significant food reserve for filter-feeding benthos, e.g., oysters (Dupuy et al. 1999; Loret et al. 2000).

In addition, phagotrophic protists consume other heterotrophic protists. The 'microbial loop' concept (Azam et al. 1983; Ducklow 1983) was based, in part, on the idea that larger protists consumed bacterivorous flagellates. Heterotrophic dinoflagellates and ciliates have since been shown to readily ingest heterotrophic flagellates as well as phytoplankton prey (Verity 1991; Solic & Krstulovic 1994; Jurgens et al. 1996). This trophic link in aquatic microbial food webs, although in theory quite important, has, to date, received surprisingly little attention. By virtue of their extracellular feeding strategies, some phagotrophic dinoflagellates, such as *Protoperidinium* sp., are also able to feed on larger-sized heterotrophic prey, includ-

ing other dinoflagellates, ciliates, and even copepod eggs and nauplii (Bockstahler & Coats 1993; Jacobson & Anderson 1996; Hansen 1998; Jeong 1994, 1999). Omnivory in phagotrophic protists is potentially a stabilizing factor in the structure and functioning of pelagic food webs (Strom et al. 2000).

### Modelling: systems-level consequences of oceanic trophic structure to organic carbon cycling (roles of protists as components of microbial food webs)

The feedback effects of phagotrophic protists on the fates of organic carbon in marine euphotic zones have been studied by use of conceptual and simulation models as well as by empirical tests of those models. Recent pelagic food web models explicitly include microzooplankton as consumers of bacteria and phytoplankton, and as food for mesozooplankton (e.g., Miller et al. 1991; Moloney 1992; Stone & Berman 1993; Baretta-Bekker et al. 1995; Thingstad et al. 1997; Sandberg et al. 2000; Tett & Wilson 2000). The proportion of phytoplankton carbon that flows through a multi-step microbial food web versus a shorter phytoplankton–mesozooplankton food chain has consequences for the capacity of marine ecosystems to sequester organic carbon or to efficiently produce fish biomass. Louis Legendre and colleagues (Legendre & Le Fevre 1995; Legendre & Rassoulzadegan 1996; Thingstad et al. 1997) have proposed theoretical scenarios in which pelagic systems characterized by an active microbial food web will export less organic carbon compared to systems in which activity of heterotrophic bacteria and protists is relatively low. However, as an empirical test of theory, Rivkin et al. (1996) described an interesting situation in a mesotrophic temperate estuary in which export flux from the water column was the same during both the spring bloom (with a smaller microbial food web) and post-bloom (with a larger, more dynamic microbial food web) although the nature of the sinking material was different. During the spring bloom the vertical flux was primarily in the form of organic aggregates composed primarily of sedimenting phytoplankton cells; during the post bloom period the major flux was in the form of fecal pellets from omnivorous copepods feeding on heterotrophic protists. Obviously, food web structure alone is not always a good predictor of the quality or quantity of sinking organic carbon. One must also include trophic flux studies coupled with hydrodynamic measurements across time and space.

It is also important to carry out studies in which data on all the major components of a pelagic ecosystem are collected simultaneously. Too often in the past, individual studies have been compartmentalized, focusing only on phytoplankton, or bacteria, or zooplankton. Recent large-scale research programs such as the JGOFS expeditions have begun to remedy this situation. In addition, smaller group projects are being carried out in regional environments, for example the U.S. Global Ocean Ecosystem Dynamics program (GLOBEC) and the European Marine Science and Technology program (MAST).

In addition, the central role of phagotrophic protists in pelagic food webs means that it is critical to obtain information on the physiological capabilities of heterotrophic flagellates, ciliates, and dinoflagellates under natural conditions, for use in construction of ecosystem models. Research on cell-specific rates of heterotrophic protists is a long-standing theme in this field that continues to the present with studies on protist feeding and growth rates (e.g., Weisse 1997; Strom & Morello 1998; Wallberg et al. 1999; Jurgens & Simek 2000; Montagnes & Weisse 2000, this volume), growth efficiencies (Straile 1997), cell carbon content (Menden-Deuer & Lessard 2000), and excretion rates of nitrogen and phosphorus nutrients (Dolan 1997).

#### **Significance of protistan predation at the community level**

A number of qualitative effects of selective grazing by protists on prey populations have been identified. In freshwater, a common result of protist grazing on bacteria is outgrowth of filamentous bacterial cells that the protists apparently cannot effectively ingest (Jurgens & Gude 1994; Jurgens et al. 1999; Posch et al. 1999; Simek et al. 1999; Hahn & Hofle 2001; Weisse this volume). This response is not usually observed in marine bacterioplankton subjected to protist grazing, although perhaps the appropriate experiments have not been done. Instead, marine bacterivorous protists selectively graze larger-sized, motile, and actively growing cells in the bacterial assemblage (Gonzalez et al. 1990; Sherr et al. 1992; Gonzalez et al. 1993a; del Giorgio et al. 1996). Bacterivorous protists can alter the phylogenetic composition of bacterial assemblages. Van Hannen et al. (1999), using a continuous culture system, showed that protist grazing was responsible for a large change in bacterial community structure as analysed by DGGE patterns. Jurgens et al

(1999) reported that in a freshwater system, the filamentous bacteria that grew up in the presence of protist grazers were  $\gamma$ - and  $\alpha$ -*Proteobacteria*, while bacteria in the beta subdivision of *Proteobacteria*, as well as some strains in the *Cytophaga-Flavobacterium* cluster, remained as small cocci and rod-shaped cells, and were rapidly grazed by flagellates. Hahn & Hofle (2001) found that flagellate grazing stimulated the growth of two freshwater *Flectobacillus* spp. in culture, thereby promoting the development of filamentous forms in these bacteria. In a mesotrophic reservoir, there were seasonal differences in the phylogenetic types of filamentous bacteria that grew up in the presence of bacterivores (Simek et al. 1999). Protists can also differentially graze phylogenetic groups of bacteria that are not so morphologically distinct. Suzuki (1999) carried out size fractionation experiments in which he demonstrated that marine bacterioplankton subject to grazing did not show a shift in phylogenetic composition, but when grazing was relieved,  $\gamma$  *Proteobacteria* increased proportionally in abundance. Lavrentyev et al. (1997) presented evidence that bacterivorous flagellates could dramatically affect the rate of nitrification in aquatic systems by consuming nitrifying bacteria, which are somewhat larger in size than most bacterioplankton, and should be subject to size-selective grazing pressure by nanoflagellates.

Selective feeding by herbivorous protists has also been reported (Verity 1991a,b). Of particular interest in regard to protist feeding on specific taxa of phytoplankton is the ability of protists to consume algal species that form harmful blooms in coastal waters. Jeong & Latz (1994) and Jeong et al. (1999a,b) reported that a heterotrophic dinoflagellate, *Protoperidium* sp., a marine ciliate, *Strombidinopsis* sp., and a mixotrophic dinoflagellate, *Fragilidium* cf. *mexicanum*, were able to grow on a number of species of red tide and toxic dinoflagellates. Kamiyama et al. (2000) observed growth of the mixotrophic dinoflagellate *Gymnodinium sanguineum* during a bloom of the toxic alga *Heterosigma akashiwo* in a bay in Japan, likely due to a predator-prey relationship between the two species. Caron et al. (1989) and Liu and Buskey (2000) have investigated the ability of pelagic protists to feed on blooms of a 2- $\mu$ m-sized 'brown tide' pelagophyte alga.

### Chemical communication between prey and predator

At the frontier of research on free-living protists in natural food webs is the study of chemically mediated interactions between predator and prey. Such interactions include the capacity of phagotrophic protists to chemically sense, and congregate at, aggregations of their prey (Fenchel & Blackburn 1999). Protist feeding rates can be affected by characteristics of prey particles such as electrostatic charge (Hammer et al. 1999) and exopolymer secretions (Liu & Buskey 2000). Most exciting are observations that prey cells can react to the presence of grazers in ways that reduce predation (Wicklow 1997). For example, Kolaczyk & Wiackowski (1997) found that a ciliate reacted to an omnivorous ciliate predator by changing cell shape so as to make it more difficult to ingest. Wolfe et al. (1997) demonstrated that specific strains of the DMS-producing alga, *Emiliana huxleyi*, showed a predator-induced chemical defense, intracellular enzymatic lysis of DMSP to the volatile gas DMS plus acrylate, that apparently deterred the protist grazers. Wolfe (2000) recently summarized the basis of chemical defense strategies in marine microbial food webs, and has pointed out promising future directions in this emerging field.

### Conclusions, and future of the field

The study of predation by free-living protists in aquatic ecosystems is still a relatively new field of research. Despite the increasingly recognized importance of phagotrophic protists in aquatic food webs, there is still a relative dearth of researchers working specifically on this category of organisms. As an example of this 'project deficit', we categorized the 45 biologically oriented research projects listed in a set of 120 recent PhD dissertation titles published by the ASLO DIALOG Program (ASLO Bulletin, June 2001). Of these projects, 13 had to do with phytoplankton, 13 with zooplankton (rotifers to krill), 10 with heterotrophic bacteria, eight with fish, and only one with heterotrophic protists. This lone thesis project was carried out by a European student (Boenigk 2000); the topic was prey selection by bacterivorous nanoflagellates. Thus, even though there is abundant evidence for the quantitative, and likely qualitative, significance of protistan herbivory in pelagic systems, in this large pool of recent doctorates in oceanography

and limnology, there was not one who had worked on herbivorous protists.

The frontiers of this field are many and obvious. We need to know specifics about phagotrophic protists as they exist *in situ*. Many studies of protists have been based on laboratory studies of cultured species that grow well at prey concentrations orders of magnitude higher than typical of most pelagic ecosystems. Studies of feeding and growth rates under natural conditions are required. Application of new methodologies, for example flow cytometry, should facilitate such studies (Weisse, this volume). Intricacies of predator-prey relationships, e.g., by chemical communication, remain to be discovered (Wolfe 2000). Molecular genetic techniques have only recently been applied to determine the phylogenetic diversity and relationships of free-living protists in aquatic ecosystems, and to identify changes in abundance of particular species of protists (e.g., Rice et al. 1997; Caron et al. 1999; Lim et al. 1999). A large number of strains of culturable heterotrophic flagellates have been isolated in marine systems (Vors 1992a,b; Lee & Patterson 1998; Tong et al. 1998; Bernard et al. 2000; Brandt & Sleight 2000), but it is very likely that this is only a small part of total flagellate diversity. Recent analysis of DNA extracted from picoeukaryotic cells in surface seawater has yielded evidence for abundant diversity, with a number of gene clones that may be affiliated with heterotrophic protists (Diez et al. 2001a,b; Moon-van der Staay et al. 2001). Using DGGE analysis, Rasmussen et al. (2001) have found a high diversity in just one group of protists – the kinoplastids, with many previously unknown gene sequences. Aquatic heterotrophic flagellates include the smallest eukaryotic cells in existence: cells smaller than 2  $\mu\text{m}$  in size. Some of these species are being isolated and identified (e.g., Karpov et al. 1998; Guillou et al. 1999b). Studies of single species as well as of communities of phagotrophic protists will undoubtedly yield new and important insights into the structure and functioning of aquatic ecosystems.

We conclude with a quote from the first serious microscopist, and the discoverer of microbes, whose philosophy of scientific research (and reporting results) is well worth emulating: 'My work, which I've done for a long time, was not pursued in order to gain the praise I now enjoy, but chiefly from a craving after knowledge, which I notice resides in me more than in most other men. And therewithal, whenever I found out anything remarkable, I have thought it my duty to put down my discovery on paper, so that all ingeni-

ous people might be informed thereof,' Antony van Leeuwenhoek, from a letter of 12 June 1716.

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