Phagotrophic Protists: Central Roles in Microbial Food Webs

Evelyn B. Sherr and Barry F. Sherr

Overview

Protists, single-celled eukaryotes, the vast majority of which are between about 2 and 200 μm in size, are ubiquitous in marine and freshwater ecosystems. Initial grouping of microbial eukaryotes into phototrophs (algae), and heterotrophs (protozoa), has morphed into categorization of protists based on molecular genetic lineage trees (Caron et al. 2012). Many non-pigmented flagellates are closely related to photosynthetic species, photosynthetic flagellates have been demonstrated to ingest bacteria or other prey (Zubkov and Tarran 2008), and acquisition of functional chloroplasts from ingested algae is common among ciliates and dinoflagellates (Flynn et al. 2012; Stoecker et al. 2009). Commonly studied aquatic protists are algae in the phytoplankton, non-pigmented, phagotrophic flagellates in the nanoplankton (2–20 μm) size class, and phagotrophic protists (microzooplankton), mainly ciliates and non-pigmented dinoflagellates, in the microplankton (20–200 μm) size class (Sieburth et al. 1978). Microzooplankton have been shown to be significant consumers of photosynthetic microbes in the sea (Calbet and Landry 2004). Our own research has focused primarily on phagotrophic nanoflagellates and microzooplankton (examples shown in Fig. 1). Here we review method development and research findings that underpin the current understanding of the roles of protists in aquatic food webs, highlighting our own work in this field. Discovering the importance of phagotrophic protists in planktonic food webs was a crucial part of the history of marine microbial ecology (Sherr and Sherr 2008).

E.B. Sherr (✉) • B.F. Sherr
College of Earth, Atmospheric and Ocean Sciences, Oregon State University, Corvallis, OR, USA
e-mail: sherre@coas.oregonstate.edu

P.M. Glibert, T.M. Kana (eds.), *Aquatic Microbial Ecology and Biogeochemistry: A Dual Perspective*, DOI 10.1007/978-3-319-30259-1_1

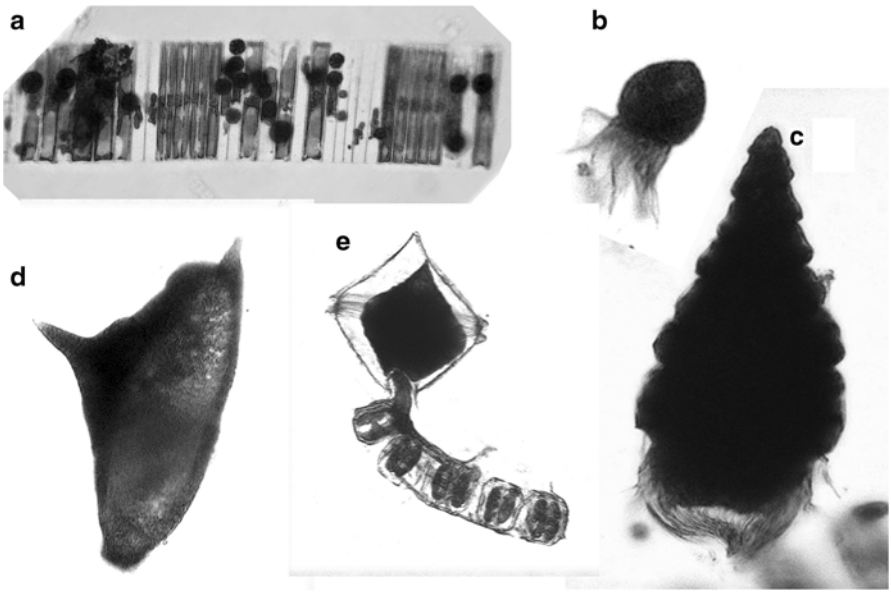

Fig. 1 Examples of protists observed in various marine systems during our career: (**a**) Parasitoid flagellates (4–6 μm) feeding on cells of a pennate diatom chain in the Bering Sea; (**b**) small spirotrichous ciliate (20×25 μm) in the plankton of the Bering Sea; (**c**) large mixotrophic ciliate, *Laboea spiralis* (50×110 μm) in the plankton of the Bering Sea; (**d**) non-thecate heterotrophic dinoflagellate, *Gyrodinium* sp. (60×90 μm), cell shape greatly distorted with an ingested pennate diatom cell, in the plankton of the coastal Oregon upwelling system; (**e**) thecate dinoflagellate, *Protoperidinium* sp. (50×60 μm) feeding extracellularly on a centric diatom chain with an extruded pseudopodial pallium in the plankton of the Bering Sea

Protists as Elemental Recyclers

The reviews of Pomeroy (1974), Azam et al (1983), and Ducklow (1983) advanced the idea that in the sea (and by implication in freshwaters as well) bacteria and their protist grazers were responsible for the bulk of ecosystem respiration and thus recycling of organic matter. Investigations of respiration and nutrient regeneration in marine habitats demonstrated that a multistep microbial food web was necessary for complete remineralization of nitrogen and phosphorus from the organic compounds in bacterial biomass.

While rates of respiration could, with caveats, be determined in seawater samples by measuring the rates of decrease of dissolved oxygen, rates of nutrient release in such experiments were too low to be accurately quantified using standard chemical analyses. Phosphate regeneration could be sensitively assessed by short-term release of radioactive P into the dissolved fraction from organic matter produced by bacteria and phytoplankton grown with added ^{32}P. However, the longest-lived radioactive form of nitrogen, ^{13}N, with a half-life of about 10 min, could not be easily used to evaluate rates of nitrogen remineralization.

Harrison (1978) and Glibert et al. (1982) pioneered the ^{15}N isotope dilution technique, in which ^{15}N labeled ammonium was added to aliquots of seawater. Seawater samples were either whole (unfiltered) or size fractioned by passing water through mesh netting or filters of progressively smaller pore size. Experimental seawater treatments with added ^{15}N ammonium were incubated under in situ conditions of light and temperature for 12–24 h. During that time, a portion of the added ^{15}N ammonium would be incorporated into phytoplankton and bacterial biomass, while the unenriched nitrogen present in organic matter would be remineralized into the pool of ammonium in the seawater. Quantitative extraction of ammonium from experimental water samples at initial and final times of incubation, followed by measurement of the ^{15}N:^{14}N isotope ratios of the extracted ammonium, allowed estimation of the extent to which the time zero ^{15}N ammonium was diluted with unenriched recycled ammonium. Harrison's initial results documented that organisms less than 35 μm in size, including bacteria and heterotrophic protists, were responsible for about 90 % of the rate of ammonium regeneration in the coastal systems that he studied. This clever, although challenging, approach was used by investigators to establish the impact of bacteria and their grazers in nutrient recycling in other aquatic systems (Glibert et al. 1992). Additional investigations focused on the amount of regeneration of nutrients by protists feeding on bacterial and phytoplankton prey with a range of C:N and C:P ratios (Caron and Goldman 1988).

Our own contribution to protist regeneration of N and P nutrients occurred at the beginning of our work as a team, during our collaboration with Tom Berman on microbial activity in Lake Kinneret, Israel from 1979 to 1981. Research on heterotrophic protists, especially bacterivorous flagellates, was cutting edge at that time, stimulated by the work on significance of protists in nutrient regeneration and by studies of Tom Fenchel on bacterivorous flagellates in Danish coastal waters (Fenchel 1982). Berman introduced us to another Israeli ecologist, Utsa Pollinger, who told us that during the decline phase of an annual dinoflagellate bloom in the lake, there was a secondary burst of tiny non-pigmented flagellates. She wondered what caused these heterotrophic flagellates to grow up. We experimented with lake water containing both bacteria and flagellates to which we added dried dinoflagellates collected from a previous year's bloom. The dinoflagellate armor plating, the theca, was composed of sugary carbohydrate that the lake bacteria readily used as a substrate. Bacterivorous flagellates then grew up, consuming the bacteria and releasing ammonium and phosphate into the water that the bacteria could use for further growth (Sherr et al. 1982). We also evaluated ammonium excretion rates by a heterotrophic flagellate isolated from lake water fed different species of bacteria (Sherr et al. 1983).

Later, while at Oregon State University, we supervised the M.S. thesis research of Marcelino Suzuki in which he used a ^{15}N tracer approach to sensitively measure the rate of regeneration of ammonium by grazing of marine flagellates on ^{15}N labeled bacteria (Suzuki et al. 1996). Suzuki's results corroborated the earlier findings based on the ^{15}N isotope dilution method; in his study nitrogen regeneration efficiencies from bacterial-N were 30–35 % for a one-step trophic link (bacterivorous flagellates), 60 % for 5 μm filtered seawater (bacterivorous flagellates plus small flagellate predators), and 90 % for unfiltered seawater with an intact microbial food web.

Phagotrophic nanoflagellates that can participate in nutrient recycling also include parasitoid flagellates that either internally infect host cells (Guillou et al. 2008; Siano et al. 2011) or feed externally on diatoms (Fig. 1a) (Tillmann et al. 1999; Sherr et al. 2013).

Protists as Consumers of Bacteria

The discovery in the 1980s of the true abundance of heterotrophic bacteria in marine and freshwaters by using fluorescent dyes to visualize bacteria with epifluorescence microscopy, coupled with measurement of rates of bacterial biomass production via incorporation of radiolabeled thymidine and leucine (Sherr and Sherr 2008), turned attention to the processes controlling bacteria growth in aquatic systems. It was obvious that heterotrophic nanoflagellates were effective grazers of the small-sized bacterial cells present in seawater (Sieburth 1981, Fenchel 1982; Andersen and Fenchel 1985). However, approaches were needed both to accurately enumerate the in situ abundances of heterotrophic flagellates, and to determine their rates of bacterial consumption. Fluorescent dyes, notably acridine orange (AO) and DAPI, already used to enumerate aquatic bacterioplankton, were applied to determining abundance of non-pigmented flagellates (Sherr et al. 1993). UV-excited, blue fluorescing DAPI was judged to be superior to blue light-excited, green fluorescing dyes such as AO, as blue-fluorescing cells made it easier to distinguish heterotrophic flagellates from chloroplast-bearing phytoflagellates.

Development of standard methods to quantify rates of flagellate bacterivory in aquatic systems proved more difficult. A variety of approaches were tried, including comparative growth of bacteria in whole water and in water filtered to remove most bacterivores, dilution of whole water with particle free water to decrease abundance of bacterivores, ingestion of radiolabeled bacteria, and use of inhibitors of eukaryotic cell growth to eliminate, or at least decrease, protist grazing on bacteria (reviewed in Strom 2000). All of these methods had serious artifactual problems and/or were too time-consuming for routine measurements.

Visualizing direct ingestion of added fluorescent particles by heterotrophic flagellates was among the methods proposed. Initial efforts used plastic, bacterial-sized beads, with or without pre-treatment with an organic compound such as bovine serum albumin to minimize bead clumping and to make the beads more palatable to flagellates (Sherr and Sherr 1993; Strom 2000). Concern remained that the plastic beads were not adequate analogs for in situ bacterioplankton, and subsequent studies showed that some protist species did show selective preference for ingestion of bacterial cells compared to bacterial-sized beads.

With help from colleagues, including our Israeli mentor Tom Berman, we developed a method to concentrate and then stain estuarine bacteria with the green fluorescing dye DTAF (Sherr et al. 1987). Known abundances of fluorescently labeled bacteria (FLB) were added to subsamples of coastal water. Flagellates in the samples fed on bacteria, including FLB, and after a short incubation time (15–60 min) ali-

quots of the incubated water were preserved and processed for microscopy. By switching epifluorescence filter sets between UV light for DAPI-stained protists, and blue light for DTAF-stained FLB, ingested FLB could be visualized inside the flagellates. After determining the average number of FLB per flagellate, and the abundances of flagellates, FLB, and total bacteria in the sample, an estimate of the rate of clearance of bacteria by flagellates could be made. This approach proved to be fairly robust, and was subsequently applied in other aquatic systems. The main consumers of bacterioplankton proved to be flagellates less than 5 μm in size (Sherr and Sherr 1991). Results of FLB ingestion and other methods of estimating rates of protist bacterivory demonstrated that this source of mortality could crop a large fraction of bacterial production in both oligotrophic as well as coastal and estuarine waters (Strom 2000). Selective ingestion by flagellates of larger-sized and metabolically active bacteria was also documented (Sherr et al. 1992; Gonzalez et al. 1993; Strom 2000).

In our bacterivory experiments, we discovered that ciliates in coastal water also ingested FLB (Sherr and Sherr 1987; Sherr et al. 1989). Marine ciliates in the plankton were thought to feed on algal cells, not bacteria. But most of the bacteria-ingesting ciliates were tiny, some only 10–12 μm in diameter (Sherr et al. 1986a). In a review of our 1986 manuscript, Tom Fenchel stated that the existence of a 10 μm-sized ciliate was as incredible as that of a 1 cm-sized mammal. We rebutted that a newborn pigmy shrew was about 1 cm long; our paper was published.

Protists as Consumers of Phytoplankton

The role of aquatic protists in marine food webs as herbivores, consumers of photosynthetic cells, is quantitatively more significant than is protistan bacterivory. This fact is a consequence of the greater biomass of photosynthetic bacteria and algae compared to the biomass of heterotrophic bacteria in both coastal and open ocean systems, and of the capacity of protists, from nanoflagellates to microzooplankton, to consume a wide range of sizes of photosynthetic cells (Sherr and Sherr 1992, 1994, 2002, 2007, 2009).

Landry and Hassett (1982) developed the dilution assay to evaluate grazing impact of microzooplankton on phytoplankton. In this approach, whole water samples are diluted with freshly prepared particle free water to yield subsamples that range from 100 % whole water to 5 % or 10 % whole water, in order to proportionally reduce protist grazing on individual phytoplankton cells. Nutrients are added to ensure equivalent cell-specific phytoplankton growth across the dilution series, and initial chlorophyll concentration is determined. After a 24 h incubation under in situ conditions of light and temperature, each experimental dilution is sampled for final chlorophyll concentration, and phytoplankton growth rates are calculated based on change in chlorophyll from initial to final time in each treatment. Typically, there is a linear decrease of phytoplankton growth rate with amount of whole water in the samples. A plot of growth rate versus proportional amount of whole water yields a regression in which the *y*-axis intercept estimates phytoplankton growth rate in the

absence of grazing (i.e. at infinite dilution), and the negative slope is the microzooplankton grazing rate. Although various concerns about the method have been raised, and dilution experiments are time-consuming to perform, the dilution assay has been adopted as the standard approach to evaluating protistan herbivory in the sea. The results have demonstrated that microzooplankton herbivory is a major source of phytoplankton mortality in all marine regions (Sherr and Sherr 2002; Calbet and Landry 2004; Sherr et al. 2009, 2013).

Protists in High Latitude Food Webs

In 1990, the year that we moved to Oregon State University, there was still surprisingly little research on microbial plankton in the Arctic Ocean, an important and climate-sensitive region of the earth. That was about to change, and we were fortunate to get onboard with developing arctic research programs.

Together with a fellow OSU oceanographer, Pat Wheeler, we were funded to participate in the Arctic Ocean Section (AOS). Two icebreakers, the U.S. Coast Guard's Polar Sea and the Canadian Coast Guard's Louis S. St. Laurent, carried an international group of marine scientists to the North Pole, the first time that North American surface ships had reached the Pole. Our part involved assessment of the abundances of microbial eukaryotes, both photosynthetic and heterotrophic, in the central Arctic Ocean (Sherr et al. 1997). In 1997–1998, again in collaboration with Wheeler, we participated in another multi-national expedition, the Surface Heat Budget of the Arctic Ocean (SHEBA), in which we were able to follow the seasonal cycle of abundances and activity of marine microbes in the central Arctic Ocean from a Canadian icebreaker, Des Groseilliers, that drifted with the ice pack for a full year (Sherr and Sherr 2003; Sherr et al. 2003). Results from both projects demonstrated that there is a diverse and active microbial food web in the Arctic Ocean, with heterotrophic flagellates feeding on both bacteria and small algae.

In subsequent high latitude projects, we shifted our focus to microzooplankton, both as herbivores and as a food resource for copepods and krill. We had long considered this latter trophic link to be a fundamental part of aquatic food webs (Sherr et al. 1986b; Sherr and Sherr 1988). We collaborated with zooplankton ecologists: Carin Ashjian at the Woods Hole Oceanographic Institution and Robert Campbell at the Graduate School of Oceanography at the University of Rhode Island, as part of the Shelf-Basin Interactions (SBI) project in the western Arctic Ocean. During cruises on the new U.S. Coast Guard icebreaker Healy in spring and summer of 2002 and 2004, our team carried out dilution assays and mesozooplankton grazing assays using on-deck incubators. Sea ice was extensive over the shelf regions during the summer of 2002, but had melted back to the central Arctic in 2004, providing a good contrast in system conditions. There was significant microzooplankton herbivory in both years (Sherr et al. 2009), and protists in the microzooplankton were avidly consumed by zooplankton, especially smaller copepods (Campbell et al. 2009).

We worked with Ashjian and Campbell on similar research in the Bering Sea in 2008–2010. The Bering Sea Ecosystem Study (BEST) was a multi-investigator program in which fisheries scientists and oceanographers collaborated in examining the impact of extent of spring sea ice on fish and marine mammal stocks in this important region. About half of the total U.S. fish catch (including pollock, halibut and salmon as well as crabs) comes from the Bering Sea, due to the extraordinary diatom blooms that start each spring at the edge of the sea ice pack, and then follow the ice as it retreats north. These diatom blooms initially support hordes of copepods and krill that are important food for fish, and then the diatoms sediment en masse to fuel the worms and clams that nourish crabs, bottom-feeding fish, gray whales, and walrus. The concern is that as climate change intensifies, the winter extent of the ice pack will lessen, and sea ice will melt sooner in the spring, disrupting the intensity and timing of the spring diatom blooms on which Bering Sea fisheries depend.

Even though we were supposed to evaluate the effects of diminished sea ice, during the March–April cruises of 2008 and 2009 there was unusually extensive sea ice, with only early-stage diatom blooms. When the spring 2010 cruise was scheduled later in the season (May–June), we were able to sample intense open water diatom blooms. As for the findings from our SBI project in the western Arctic Ocean, the BEST data underscored the importance of both diatoms and microzooplankton to Bering Sea food webs. A clear result from both these projects was that large, non-pigmented dinoflagellates were important consumers of bloom-forming diatoms, both as single cells and chains (Sherr et al. 2009, 2013). Most investigations of microzooplankton as food for zooplankton had considered ciliates (e.g. Fig. 1b, c) as the major group of herbivorous protists. We found that in the western Arctic Ocean, in the Bering Sea, and also in upwelling diatom blooms in Oregon coastal waters, herbivorous dinoflagellates (e.g. Fig. 1d, e) often composed 50 % or more of microzooplankton biomass, and were major grazers of diatoms in the sea (Sherr and Sherr 2007; Sherr et al. 2013).

Looking to the Future

Research on the quantitative impact of phagotrophic protists on recycling and trophic transfers in aquatic ecosystems has expanded to include assessment of the genetic diversity of heterotrophic protists (Caron et al. 2012), investigation of chemical cues that affect prey ingestion (Roberts et al. 2011), and study of the biochemistry of prey detection in phagotrophic protists (Hartz et al. 2008, 2011). Results of molecular genetic studies suggest that the taxonomic diversity of both autotrophic and heterotrophic protists in marine systems is extraordinary. One interesting finding is the ubiquitous presence in the sea of protists related to a group of dinoflagellates, the Syndiniales, that parasitize other protists (Guillou et al. 2008; Siano et al. 2011). Protist parasitism is an alternate mode of predator–prey interaction that is ripe for further study; we noted parasitoid flagellates infecting diatoms in the Bering Sea (Sherr et al. 2013; Fig. 1a).

Investigation of environmental cues that affect prey detection or avoidance is another new and exciting research field (Roberts et al. 2011). The initial discovery that the metabolite dimethyl sulfide (DMS) could be released by haptophyte algae as a defense against protist predation was made by Gordon Wolfe (Wolfe et al. 1994, 1997), a post-doctoral colleague working in our laboratory at OSU. Our graduate student, Aaron Hartz (Hartz et al. 2008), subsequently demonstrated that inhibition of intracellular signal transduction pathways decreased chemosensory response to prey in a marine dinoflagellate and ciliate. He also found that the non-pigmented marine dinoflagellate, *Oxyrrhis marina*, expressed rhodopsin and could orient to various wavelengths of light. We speculated that both chemical and light signals could be used by protists to find prey in situ (Hartz et al. 2011).

Evelyn B. Sherr and Barry F. Sherr

We bonded over sewage sludge. In 1975–1977, Ev, a new research scientist at the University of Georgia Marine Institute on Sapelo Island, and Barry, a graduate student at the University of Georgia, collaborated on a project to evaluate whether salt marsh microbes could break down organic wastes and remove nitrogen via denitrification from secondarily treated sewage sludge applied to a cordgrass marsh. We asked Larry Pomeroy, who was directing a major project in the salt marshes around Sapelo, if we could borrow his research van to deliver sludge from the Athens, GA, waste treatment plant to the island. We may not have been entirely clear about what we were going to transport. After loading up the sludge in trash barrels, we drove to the coast in time for the afternoon ferry to the island. It was a warm day, and with windows open we didn't notice the winged creatures emerging from the barrels. But when we got to the coast and opened the van, a cloud of sludge flies exploded from the interior. We tried to shoo out as many flies as we could, without great success. Pomeroy later had the van fumigated. We were married in 1979, after Barry finished his Ph.D., and went to Israel for a year and a half research "honeymoon." We returned to work at the UGMI until 1990 when we relocated to Oregon State University with our two young sons. Projects in the Arctic and in the upwelling system off the Oregon coast occupied us until our retirement in 2012.

References

Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. Mar Ecol Prog Ser 10:257–263

Andersen P, Fenchel T (1985) Bacterivory by microheterotrophlc flagellates in seawater samples. Limnol Oceanogr 30:198–202

Calbet A, Landry MR (2004) Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnol Oceanogr 40:51–57

Campbell RG, Sherr EB, Ashjian CJ, Plourde S, Sherr BF, Hill V, Stockwell DA (2009) Mesozooplankton prey preference and grazing impact in the Western Arctic Ocean. Deep Sea Res II 56:1274–1289

Caron DA, Goldman JC (1988) Dynamics of protistan carbon and nutrient cycling. J Protozool 35:247–249
Caron DA, Countway PD, Jones AC, Kim DY, Schnetzer A (2012) Marine protistan diversity. Ann Rev Mar Sci 4:467–493
Ducklow HW (1983) Production and fate of bacteria in the oceans. Bioscience 33:494–501
Fenchel T (1982) Ecology of heterotrophic flagellates. IV. Quantitative occurrence and importance as bacterial consumers. Mar Ecol Prog Ser 9:35–42
Flynn K, Stoecker D, Mitra A, Raven J, Glibert P, Hansen P, Graneli E, Burkholder J (2012) Misuse of the phytoplankton-zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. J Plankton Res. doi:10.1093/plankt/fbs062
Glibert PM, Lipschultz F, McCarthy JJ, Altabet MA (1982) Isotope dilution models of uptake and remineralization of ammonium by marine plankton. Limnol Oceanogr 27:639–650
Glibert PM, Miller CA, Garside C, Roman MRR, McManus GB (1992) 14NH4+ regeneration and grazing: interdependent processes in size-fractionated 15NH4+ experiments. Mar Ecol Prog Ser 35:462–476
Gonzalez JM, Sherr EB, Sherr BF (1993) Differential feeding by marine flagellates on growing vs starving bacteria, and on motile vs non-motile bacteria. Mar Ecol Prog Ser 102:257–267
Guillou L, Viprey M, Chambouvet A, Welsh RM, Kirkham AR, Massana R, Scanlan DJ, Worden AZ (2008) Widespread occurrence and genetic diversity of marine parasitoids belonging to Syndiniales (Alveolata). Environ Microbiol 10:3349–3365
Harrison WG (1978) Experimental measurements of nitrogen remineralization in coastal waters. Limnol Oceanogr 23:684–694
Hartz AJ, Sherr BF, Sherr EB (2008) Using inhibitors to investigate the involvement of cell signaling in predation by marine phagotrophic protists. J Euk Microbiol 55:18–21
Hartz AJ, Sherr BF, Sherr EB (2011) Photoresponse in the heterotrophic marine dinoflagellate *Oxyrrhis marina*. J Eukaryot Microbiol 58:171–177
Landry MR, Hassett RP (1982) Estimating the grazing impact of marine microzooplankton. Mar Biol 67:283–288
Pomeroy LR (1974) The ocean's food web: a changing paradigm. Bioscience 24:499–504
Roberts EC, Legrand C, Steinke M, Wootton EC (2011) Mechanisms underlying chemical interactions between predatory planktonic protists and their prey. J Plankton Res 33:833–841
Sherr EB, Sherr BF (1987) High rates of consumption of bacteria by pelagic ciliates. Nature 325:710–711
Sherr EB, Sherr BF (1988) Role of microbes in pelagic food webs: a revised concept. Limnol Oceanogr 33:1225–1227
Sherr BF, Sherr EB (1991) Proportional distribution of total numbers, biovolume, and bacterivory among size classes of 2-20 mm nonpigmented marine flagellates. Mar Microb Food Webs 5:227–237
Sherr EB, Sherr BF (1992) Trophic roles of pelagic protists: phagotrophic flagellates as herbivores. Arch Hydrobiol Beih 37:165–172
Sherr EB, Sherr BF (1993) Protistan grazing rates via uptake of fluorescently labeled prey. In: Kemp P, Sherr B, Sherr E, Cole J (eds) Current methods in aquatic microbial ecology. Lewis Publ, NY, pp 695–702
Sherr EB, Sherr BF (1994) Bacterivory and herbivory: key roles of phagotrophic protists in pelagic food webs. Microb Ecol 28:223–235
Sherr EB, Sherr BF (2002) Significant of predation by protists in aquatic microbial food webs. Anton Leeuw Int J G Mol Microbiol 81:293–308
Sherr BF, Sherr EB (2003) Community respiration/production and bacterial activity in the upper water column of the central Arctic Ocean. Deep Sea Res I 50:529–542
Sherr EB, Sherr BF (2007) Heterotrophic dinoflagellates: a significant component of microzooplankton biomass and major grazers of diatoms in the sea. Mar Ecol Prog Ser 352:187–197
Sherr EB, Sherr BF (2008) Understanding roles of microbes in marine pelagic food webs: a brief history (Chapter 2). In: Kirchman D (ed) Microbial ecology of the oceans, 2nd edn. Wiley, New York, NY, pp 27–44

Sherr EB, Sherr BF (2009) Role of herbivorous protists in controlling initiation and development of marine phytoplankton blooms. Aquat Microb Ecol 57:253–262
Sherr BF, Sherr EB, Berman T (1982) Decomposition of organic detritus: a selective role for microflagellate protozoa. Limnol Oceanogr 27:765–769
Sherr BF, Sherr EB, Berman T (1983) Grazing, growth, and ammonia excretion rates of a heterotrophic microflagellate fed four species of bacteria. Appl Environ Microbiol 45:1196–1201
Sherr EB, Sherr BF, Fallon RD, Newell SY (1986a) Small aloricate ciliates as a major component of the marine heterotrophic nanoplankton. Limnol Oceanogr 31:177–183
Sherr EB, Sherr BF, Paffenhofer G (1986b) Phagotrophic protozoa as food for metazoans: a "missing" link in marine pelagic food webs? Mar Microb Food Webs 1:61–80
Sherr BF, Sherr EB, Fallon RD (1987) Use of monodispersed, fluorescently labeled bacteria to estimate in situ protozoan bacterivory. Appl Environ Microbiol 53:958–965
Sherr BF, Rassoulzadegan F, Sherr EB (1989) Bacterivory by pelagic choreotrichous ciliates in coastal waters of the NW Mediterranean Sea. Mar Ecol Prog Ser 55:235–240
Sherr BF, Sherr EB, McDaniel J (1992) Effect of protistan grazing on the frequency of dividing cells (FDC) in bacterioplankton assemblages. Appl Environ Microbiol 58:2381–2385
Sherr EB, Caron DA, Sherr BF (1993) Staining of heterotrophic protists for visualization via epifluorescence microscopy. In: Kemp P, Sherr B, Sherr E, Cole J (eds) Current methods in aquatic microbial ecology. Lewis Publ, New York, NY, pp 213–228
Sherr EB, Sherr BF, Fessenden L (1997) Heterotrophic protists in the central Arctic Ocean. Deep Sea Res II 44:1665–1682
Sherr EB, Sherr BF, Wheeler PA, Thompson K (2003) Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. Deep Sea Res I 50:557–571
Sherr EB, Sherr BF, Hartz AJ (2009) Microzooplankton grazing impact in the Western Arctic Ocean. Deep Sea Res II 56:1264–1273
Sherr EB, Sherr BF, Ross C (2013) Microzooplankton grazing impact in the Bering sea during spring sea ice conditions. Deep Sea Res II 94:57–67
Siano R, Alves-de-Souza C, Foulon E, Bendif EM, Simon N, Guillou L, Not F (2011) Distribution and host diversity of Amoebophryidae parasites across oligotrophic waters of the Mediterranean Sea. Biogeosciences 8:267–278
Sieburth JNM (1981) Protozoan bacterivory in pelagic marine waters. In: Hobbie PJB (ed) Heterotrophic activity in the sea. Plenum, New York, NY, pp 405–444
Sieburth JMN, Smetacek V, Lenz J (1978) Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. Limnol Oceanogr 23:1256–1263
Stoecker DK, Johnson MD, de Vargas C, Not F (2009) Acquired phototrophy in aquatic protists. Aquat Microb Ecol 57(3):279–310
Strom SL (2000) Bacterivory: interactions between bacteria and their grazers. In: Kirchman DL (ed) Microbial ecology of the oceans. Wiley-Liss, New York, pp 351–386
Suzuki MT, Sherr EB, Sherr BF (1996) Estimation of ammonium regeneration efficiencies associated with bacterivory in pelagic food webs via a ^{15}N tracer method. J Plankton Res 18: 411–428
Tillmann U, Hesse K-J, Tillmann A (1999) Large-scale parasitic infection of diatoms in the Northfrisian Wadden Sea. J Sea Res 42:255–261
Wolfe GV, Sherr EB, Sherr BF (1994) Release and consumption of DMSP from *Emiliania huxleyi* during grazing by *Oxyrrhis marina*. Mar Ecol Prog Ser 111:111–119
Wolfe GV, Steinke M, Kirst GO (1997) Grazing-activated chemical defence in a unicellular marine alga. Nature 387:894–897
Zubkov MV, Tarran GA (2008) High bacterivory by the smallest phytoplankton in the North Atlantic Ocean. Nature 455:224–226