

## Oceanic Protists

BY BARRY F. SHERR, EVELYN B. SHERR, DAVID A. CARON, DANIEL VAULOT, AND ALEXANDRA Z. WORDEN

Protists are microscopic eukaryotic microbes that are ubiquitous, diverse, and major participants in oceanic food webs and in marine biogeochemical cycles. The study and characterization of protists has a long and distinguished tradition. Even with this history, the

form massive blooms that can be seen from space. However, during nonbloom seasons, even smaller cells (picoplankton—prokaryotes and eukaryotes less than a few micrometers in size) typically dominate phytoplankton biomass and production (Li, 2002; Worden et al.,

organisms for nutrition. Most are phagotrophic—they ingest prey—usually other microbes. Some heterotrophic protists are parasites of phytoplankton (Kuhn et al., 2004) or zooplankton (Théodorides, 1987), while still others form symbiotic relationships with autotrophic or heterotrophic bacteria (Foster et al., 2006; Guillou et al., 1999). In addition, many species of protists have mixed trophic modes. These “mixotrophs” include flagellated phytoplankton that ingest bacteria or other protists (Caron, 2000), ciliates that “farm” chloroplasts from ingested algal prey (Stoecker, 1992), and mutualistic relationships between photosynthetic microorganisms and heterotrophic protists (Caron and Swanberg, 1990). Heterotrophic nutrition occurs among virtually all lineages of protists. Some protistan groups formerly classified as “algae” include species with strictly heterotrophic nutrition. For example, the dinoflagellates include many heterotrophic species (Lessard,

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extraordinary species diversity and variety of interactions of protists in the sea are only now being fully appreciated. Figure 1 shows representative examples of marine protists, and of methods used to visualize these microbes.

Protists can be autotrophic or heterotrophic. The former, also called microscopic algae, contain chloroplasts, thrive by photosynthesis, and are at the base of all oceanic food webs, with the exception of deep-sea chemosynthetic ecosystems. There is a general trend for > 20- $\mu\text{m}$  sized phytoplankton (microplankton), such as diatoms and dinoflagellates, to dominate episodically in coastal waters, while in the open ocean 2–20- $\mu\text{m}$  sized cells (nanoplankton), such as coccolithophorids, sporadically

2004). Some genera of marine picoalgae can “bloom” to very high concentrations (>  $10^5$  cells  $\text{ml}^{-1}$ ), *Ostreococcus* (Countway and Caron, 2006), while others are ubiquitous, such as *Micromonas*, which is found from arctic to tropical waters (Not et al., 2004; Worden, 2006).

In contrast to photosynthetic protists, heterotrophic protists have no permanent chloroplasts and rely on other

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BARRY F. SHERR ([sherrb@coas.oregonstate.edu](mailto:sherrb@coas.oregonstate.edu)) is Professor, College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA. EVELYN B. SHERR is Professor, College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA. DAVID A. CARON is Professor, Department of Biological Sciences, University of Southern California, Los Angeles, CA, USA. DANIEL VAULOT is Directeur de Recherche at the Station Biologique de Roscoff, UMR 7144 CNRS and Université Pierre et Marie Curie, France. ALEXANDRA Z. WORDEN is Assistant Professor, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL, USA.

1991; Jeong, 1999), and it is possible that all dinoflagellates, including the photosynthetic species responsible for red tides, may have the capacity for phagotrophy (H.J. Jeong, Seoul National University, *pers. comm.*, July 2006).

Phagotrophic protists have long been known to be important in oceanic food webs as consumers of bacteria and phytoplankton (reviewed in Strom, 2000; Sherr and Sherr, 2002; Calbet and Landry, 2004), as regenerators of nutrients for further phytoplankton growth (Caron and Goldman, 1990), and as a food resource for marine zooplankton (Stoecker and Capuzzo, 1990). The grazing impact of phagotrophic protists has consequences for both ecosystem modeling and for the structure of microbial communities. The proportion of organic carbon produced by phytoplankton that flows through a multi-step microbial food web versus a shorter phytoplankton-mesozooplankton food chain is a critical factor that determines the capacity of marine ecosystems to sequester organic carbon and to efficiently produce fish biomass (Legendre and Le Fevre, 1995). Via selective grazing, both herbivorous and bacterivorous protists can alter the community composition of oceanic phytoplankton (Strom and Loukos, 1998) and bacterial assemblages (Suzuki, 1999; Jurgens and Matz, 2002). It is clear that these activities constitute major roles in oceanic ecosystems, and considerable information has been amassed on the abundances, distributions, and ecological roles of protists, yet there is still much to learn. At present, much of our knowledge is restricted to larger species that have readily identifiable morphological traits

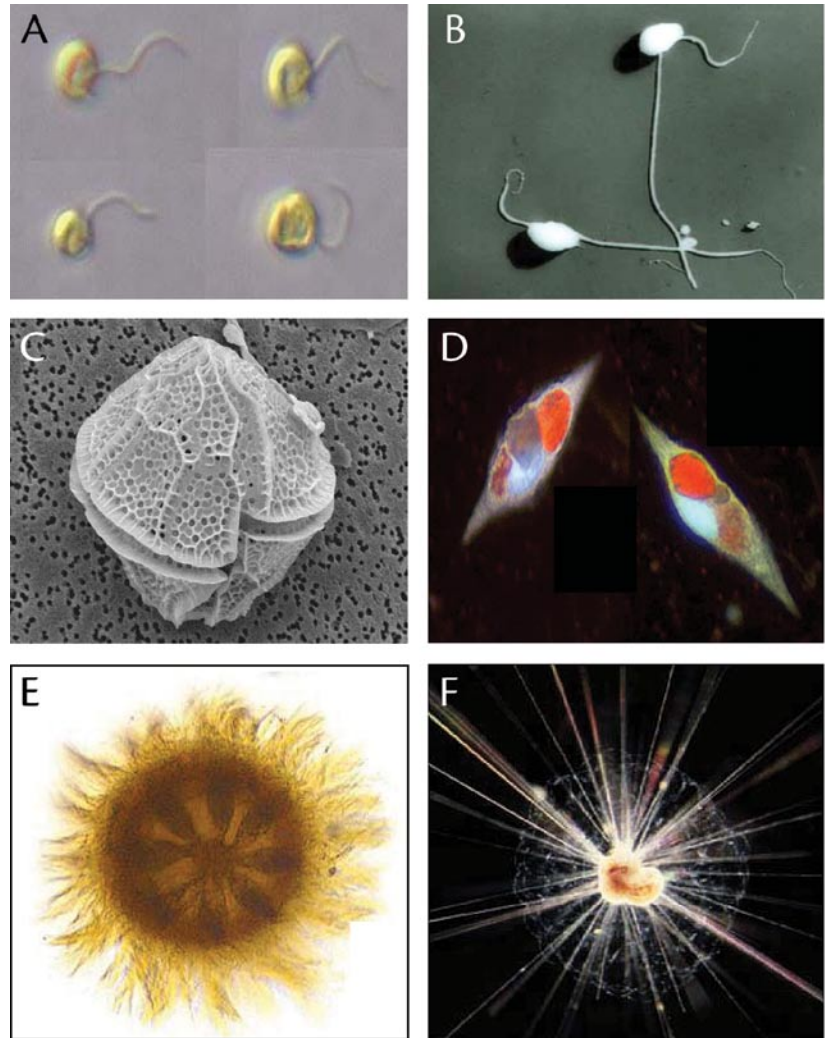


Figure 1. Examples of marine protists and of methods used to visualize eukaryotic microbes: (A) Live cells of the 2- $\mu\text{m}$ -diameter marine flagellated alga *Pelagomonas calceolate*, transmitted light microscopy. (B) Two cells of a 5- $\mu\text{m}$ -long marine heterotrophic flagellate (*Bodo* sp.), scanning electron microscopy (SEM). (C) A 50- $\mu\text{m}$ -diameter autotrophic thecate dinoflagellate (*Lingulodinium polyedrum*) that forms red tide blooms, SEM. (D) Two cells of a 20  $\times$  60  $\mu\text{m}$  marine heterotrophic dinoflagellate (*Gyrodinium* sp.) with food vacuoles full of ingested coccoid cyanobacteria, epifluorescence microscopy after preservation with formaldehyde and staining with the fluorochrome DAPI. (E) The 55- $\mu\text{m}$ -diameter marine pelagic ciliate *Strombilidium* sp., inverted light microscopy after preservation with acid Lugol fixative. (F) Live foraminiferan *Hastigerina pelagica* with a fluid bubble capsule and a test approximately 300  $\mu\text{m}$  across, darkfield light microscopy. Sources of micrographs: (A) culture collection of the Station Biologique Roscoff ([planktonnet.sb-roscoff.fr](http://planktonnet.sb-roscoff.fr)); (B) laboratory of John Sieburth, courtesy of Dave Caron; (D) and (E) B. and E. Sherr; (C) and (F) Dave Caron

and those species that are amenable to laboratory culture.

One fundamental question that has become a focus of research and debate in recent years revolves around the species concept (and species boundaries) for protists. Although protistan species have traditionally been defined based on their morphology, recent molecular analyses and physiological studies reveal that even well-defined morphospecies may be composed of a mosaic of multiple genetic/physiological types. For instance, the ubiquitous diatom *Skeletonema costatum*, thought until recently to be a single species, is actually a composite of ten genetic types that are now considered distinct species (Zingone et al., 2005; Sarno et al., 2005). Similarly, physiological variability among *Spumella*-like heterotrophic flagellates indicates geographically distinct adaptations and emphasizes that morphology needs to be complemented by other approaches for distinguishing different species (Boenigk et al., 2006). The situation is even more

late (Groissillier et al., 2006) and stramenopile (Massana et al., 2006) divisions have escaped detection until recently. The discovery of many cryptic lineages highlights the importance of combining molecular and ecological information with traditional morphological descriptions. This combination facilitates meaningful investigation of the distribution and activities of marine protists in situ (Modeo et al., 2003).

These new approaches for defining protistan species have energized an ongoing debate regarding protistan species diversity and biogeography. The overarching question is whether there are relatively few species of protists that are broadly distributed, or whether similar protistan morphotypes are in fact distinct species or subspecies with more limited distribution (Fenchel, 2005; Katz et al., 2005). Why does species diversity matter? From an ecological perspective, it is important to know what taxonomic level (e.g., species or subspecies) yields information about associated differ-

graphically restricted gene flow) among species of ciliates in isolated tide pools. Little is known at this juncture about the distribution, gene flow, diversity, ecological roles, or even the morphologies of the previously undescribed lineages of protists now being revealed by molecular analyses.

Beyond characterizing the diversity and distribution of protists in the ocean, major lines of research continue to elucidate the ecological roles of protists in marine ecosystems. Species-specific growth, grazing, and nutrient excretion rates of heterotrophic protists are derived mainly from laboratory experiments using isolated species fed monospecific prey under conditions that poorly mimic natural systems. However, such studies show that phagotrophic protists exhibit various types of species-specific behavior that may affect feeding behavior and growth, including chemosensory responses to prey and selective ingestion of prey types (Strom, 2000; Wolfe, 2000). In turn, prey cells may use structural or chemical defenses against protistan predation (Wolfe, 2000; Jurgens and Matz, 2002; Matz et al., 2004). Research on the underlying physiological/biochemical basis of the feeding behavior of marine protists is yielding new awareness and understanding of their predator-prey interactions (Wolfe, 2000; Wooten et al., 2006). The ability of herbivorous protists to discriminate between alternate prey types depending on size and “taste” (Verity, 1991; Hansen, 1992; Strom et al., 2003; Wooten et al., 2006) undoubtedly affects protistan grazing impact on bloom-forming phytoplankton, such as diatoms and harmful algal species (Jeong, 1999). Studies

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complicated for the tiny picoplanktonic protists in the ocean. Molecular analyses during the last ten years have revealed many undescribed and uncultivated taxa among these morphologically similar forms (Moon-van der Staay et al., 2001; López-García et al., 2001; Diéz et al., 2001), and whole lineages in the alveo-

ences in functional roles (i.e., how these organisms participate in food webs). Based on analysis of genetic variation, Katz et al. (2005) found evidence for a “cosmopolitan” distribution (high gene flow and low diversity) for species of ciliates in coastal waters and evidence for “endemism” (high diversity and geo-


of protistan herbivory on in situ phytoplankton communities indicate that food quality can play an important role in grazer selectivity (e.g., Worden and Binder, 2003) and that protistan growth efficiencies vary greatly with prey type (e.g., Guillou et al., 2001). Accurately describing the rates of activity of heterotrophic protists is extremely important to carbon-cycle models.

Unquestionably, many fascinating discoveries are ahead for protistan researchers at the physiological, organismal, and community levels. These include:

- characterizing the overall breadth and meaning of protistan species diversity in the ocean;
- understanding the ecology of minute organisms, such as the 2  $\mu\text{m}$  heterotrophic flagellate *Symbiomonas scintillans* that itself harbors an endosymbiotic bacterium (Guillou et al., 1999) and the pico-alga *Ostreococcus tauri*, the smallest free-living eukaryote known (Courties et al., 1994), which can occur at high abundances (Countway and Caron, 2006) and has unique genome features (Derelle et al., 2006);
- deciphering the ecological, molecular, and biochemical processes that might explain chloroplast acquisition by heterotrophic protists (Gast et al., in press); and
- characterizing microbial interactions and processes sufficiently to provide a predictive understanding of community function and how microbial communities will respond in the face of environmental change.

Yet another challenge ahead is to understand the importance of processes such as parasitism and symbiosis in regulat-

ing oceanic plankton community structure and production; both are known to occur (Foster, 2006), but little is known about their prevalence and extent in marine systems.

Breakthroughs will depend on the application of a diverse array of approaches and methodologies. These will almost assuredly hold implications even beyond the important roles these organisms are already known to play in oceanic ecosystems. Marine protists likely retain some characteristics of the earliest eukaryotes that evolved on Earth. Interrogation of their genomes provides insights into how they thrive in the world's ocean (Ambrust et al., 2005; Derelle et al., 2006) and insights into fundamental biological processes such as the evolution of multicellularity (King et al., 2004), and thus will foster a better understanding of the evolution of life on our planet. 

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