



FIGURE 6 The intertidal zone on the north side of Cape Blanco, Oregon. The large, smooth boulders are made of serpentine, while the surrounding rock from which the intertidal platform is formed is sandstone. The smooth boulders are from a source outside the intertidal zone and were carried into the intertidal zone by waves.

<AUG1> Photograph by.

the surrounding shore (Fig. 6). These errant boulders were transported by waves from a source outside the intertidal zone. One can imagine the destruction they must cause as waves propel them through the intertidal landscape.

Engineering studies of the failure of stone breakwaters describe the conditions under which large rocks and even boulders can be mobilized. What engineers report is that breakwaters composed of large boulders fail (i.e., the boulders are washed away) not when a storm is approaching shore and the waves are large, often the largest of a storm event, and with a long period. Rather, the breakwater fails as the storm arrives at the coast and the breakwater is subjected to large waves with short periods. As the storm approaches shore and the breakwater is hit by very large, long-period waves (swells), it is subjected to the highest wave-generated current velocities. The boulders remain in place during this phase of a storm, suggesting that the drag forces generated by the high current velocities are inadequate to mobilize boulders. As the storm hits the coast, the breakwater is impacted by large, short-period waves

(seas), and these waves can mobilize boulders. During this phase of the storm the rapid changes in current direction caused by these large, short-period waves generate high accelerative forces, and it is these forces that ultimately can move even large boulders.

Traditionally, most rocky-intertidal ecological studies have been conducted on rocky platforms where the substrate is composed of stable basement rock. Projectiles tend to be uncommon in these types of habitats, and damage from projectiles is usually light. Perhaps for this reason the role of projectiles in intertidal ecology has received little attention. Boulder-field intertidal zones are as common as, if not more common than, rock platforms. In boulder fields, projectiles are abundant, and the evidence of damage due to projectiles is obvious. Here projectiles may be one of the most important defining physical forces in the habitat.

SEE ALSO THE FOLLOWING ARTICLES

Geology, Coastal / Habitat Alteration / Hydrodynamic Forces / Wave Exposure

FURTHER READING

- Carstens, T. 1968. Wave forces on boundaries and submerged bodies. *Sarsia* 34: 37–60.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 45: 137–159.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences of the USA* 71: 2744–2747.
- Shanks, A. L., and W. G. Wright. 1986. Adding teeth to wave action: The destructive effects of wave-borne rocks on intertidal organisms. *Oecologia* 69: 420–428.
- Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49: 227–254.

PROTISTS

GERARD M. CAPRIULO

Saint Mary's College of California

JOHN J. LEE

City College of City University of New York

Prokaryotic (bacteria and cyanobacteria) as well as eukaryotic (protists; micro “algae” and “protozoa”) microorganisms abound in all of earth’s habitats from the benign to the extreme. With their fast growth and high metabolic

and respiration rates, they are important components of all ocean systems and subsystems. Protists (as well as bacteria and cyanobacteria) are integral components of marine food webs as primary producers and consumers, and as nutrient recyclers of biomass and detrital materials.

HABITATS, ECOLOGICAL CONSIDERATIONS AND THE PHYSICAL ENVIRONMENT

In the rocky intertidal zone and tidepools, protists are found as plankton; in relationship with organic and inorganic suspended particles, sediments, and rock surfaces; and as exobionts and endobionts of other organisms. In response to the dynamic and continually changing nature of the intertidal zone and tide pools, attached and trapped microorganisms must be adapted to the associated large periodic fluctuations in salinity, temperature, desiccation levels, and solar irradiance. When these habitats are marked with robust detrital decay or are isolated and characterized by high photosynthetic rates, adaptations to wide changes in pH are also necessary. Because of diffusion dynamics and their small sizes relative to the viscosity of water, protists experience the rocky intertidal zone and tidepools as a series of subdivided—but interconnected microhabitats, each one of which promotes their success or demise based on the microhabitat's individual microscale characteristics. The success of protists in intertidal rocky shores and their tidepools thus depends on their physiochemical tolerances, abilities to compete for resources, nutrient availability, the organic chemistry and molecular properties of the habitat, the presence of prokaryote microbes, and, to a major extent, substrate and sediment characteristics. For their part, tidepools can be considered islands ready to recruit “r-selected” organisms (those with high rates of reproduction and growth) as they are formed. Since colonization is stochastic, very often nearby different tide pools have blooms of different protists and different food webs of protists and micrometazoa.

Shorelines are born of past and present geological forces acting on above- and below-sea-level land masses, which are also altered by air, sea, and limnologically mediated physical and chemical (e.g., erosion, depositional forces, and chemical reactions) and biological interactions. Each shoreline has its own history and unique set of sediment properties, including particle chemical characteristics, crystalline structures, and size distribution. The latter ranges from the finest sediments (i.e., clays and muds), to sand (fine to coarse), and rocks (from gravel to smooth and jagged boulders and mountain ranges).

As tides advance and retreat, the rocky intertidal zone undergoes rhythmic variations in exposure to extreme

physical, chemical, geological, and biological factors. Because each point is exposed differently depending on its position and the slope of the shore grade, the littoral zones of rocky shores generally show more pronounced elevation gradients and associated permanent horizontal banding patterns of life forms than are found in other marine habitats. The specific distribution dynamics of life forms in these habitats vary with their respective sizes and are primarily driven by physiochemical size scale parameters.

The rocky intertidal world inhabited by microbes is very different from that which we experience. Because of their small size, bacteria and protists live life at very low Reynolds numbers. This means that viscosity plays a key role in their world. Living in the water to them is the equivalent of living in a sea of cold molasses syrup for humans. The forces the protists exert to move often are barely able to overcome the viscous forces of the water in which they live. Also, their diminutive sizes means they are much closer in size to that of the molecules they encounter. This influences their environmental directional world and their perceptions and responses to stimuli. For this reason we must carefully consider questions of scale, diffusion, micro-level habitat structures, and environmental patchiness when engaging ecological questions related to bacteria, cyanobacteria, and the protista. From this perspective, a rocky shore is, for microbial eukaryotes, much more than it appears, at first glance, to the human eye. It contains a host of unique habitats that include spray; midlittoral and infralittoral zones; tidepools; soft, hard, and porous rock zones and their associated cracks and crevices; sand and mud zones; seaweed surfaces; algal and bacterial mats; planktonic zones; detritus and dead organism remains; bird and other animal droppings; and the bodies of live organisms.

THE PROTIST PLAYERS OF ROCKY SHORES

In the late twentieth century, detailed electron microscopic and molecular genetic studies changed scientists' concepts of the phylogenetic relatedness of protist groups from earlier conceptualizations, which divided protists into “protozoa” and “algae.” At present many protist phylogenetic relationships are not neatly resolved, and many discrete, monophyletic, and often seemingly unrelated groups of protists are recognized that could be raised to the level of phyla.

Associated with rocky shoreline habitats are a plethora of both prokaryotic and eukaryotic marine microbes, many of which can be sampled relatively easily (Table 1). The protist microorganisms are an extensive, taxonomically

TABLE 1
Some Simple Techniques for Sampling the Protists of Rocky Shores and Tidepools

1. Gently grasp a small piece of seaweed, place into a test tube with filtered seawater, vigorously shake to dislodge epiphytic protist community.
2. Place a test tube close to a submerged rock and scrape a sample from the rock into the test tube.
3. For sandy or muddy benthos use a small piece of plastic tubing attached to a 5-mL or 10-mL syringe (made more quantitative by pushing a plastic ring into the benthos and then sucking the surface with the tube and syringe).
4. Recruit protists to microscope slides using a grooved rubber stopper that will hold several slides. Place on the benthos for a few days to a week, then cover one side of slide with a cover-glass, clean the other side, observe via microscopy.
5. For the water column (a) tie polyfoam sponges to a fishing line and weight the other side with a fishing sinker. The floating sponge will be colonized by the microorganisms in the water column, which are then squeezed into a beaker, or (b) pass the sample through a membrane filter (0.2 or 0.45 μm for bacteria and protists). Filters with larger pore sizes (e.g., 3 μm , 5 μm , 8 μm) can be used to selectively capture by size (note, some protists are too fragile for sampling via filtration). A hand-held vacuum pump with pressure gauge, 5 psi or less, and stopping the filtering before the membrane is dry, is recommended.
6. For special protist collections additional preparation may be necessary.

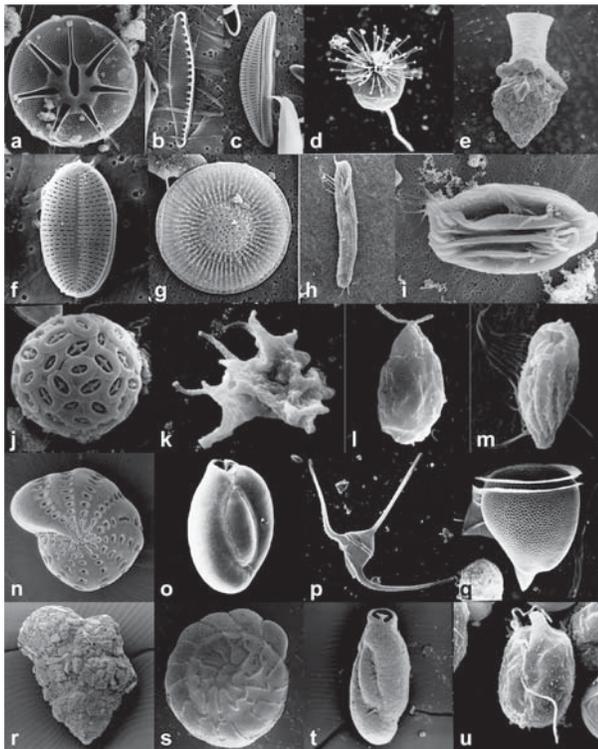


FIGURE 1 Scanning electron micrographs of a representative sampling of protist groups that inhabit rocky intertidal zones and tidepools: (A) centric diatom, *Asterophalus*, size 30 μm ; (B) pennate diatom, *Nitzschia*, size 10.5 μm ; (C) pennate diatom, *Amphora*, size 20 μm ; (D) Ciliophora, *Suctorina*, size 80 μm ; (E) Ciliophora, Spirotrichea, Tintinnida, *Codonellopsis lorica*, size 133 μm ; (F) pennate diatom, *Cocconeis*, size 9 μm ; (G) centric diatom, *Cyclotella*, size 18 μm ; (H), Ciliophora, Heterotrichea, *Condylotoma*, size 115 μm ; (I) Ciliophora, *Euplotes* (ventral side), size 40 μm ; (J), Prymnesiida, coccolithophorid, *Cruciplacolithus* (coccosphere with interlocking placoliths), size 10 μm ; (K) ramicristate amoeba, *Vexillifera*, size 34 μm ; (L) Volvocida, *Dunaliella*, size 8 μm ; (M) Ciliophora, Scuticociliatia, *Pseudocyclidium*, size 10 μm ; (N) Granuloreticulosa (Foraminifera), *Elphidium*, size 350 μm ; (O) Granuloreticulosa (Foraminifera), *Quinqueloculina*, size 160 μm ; (P) Dinozoa, *Ceratium*, size 150 μm ; (Q) Dinozoa, *Dinophysis*, size 75 μm ; (R) Granuloreticulosa (Foraminifera), *Textularia*, size 800 μm ; (S) Granuloreticulosa (Foraminifera), *Ammonia*, size 1300 μm ; (T) Granuloreticulosa (Foraminifera), *Millammina*, size 850 μm ; (U) Dinozoa, *Amphidinium*, size 20 μm . Images by

diverse group of photosynthetic and heterotrophic flagellates, nonmotile photosynthetic cells, gliding photosynthetic cells, amoebae, and ciliates. It is beyond the scope of this article to detail all of them. However, it is important to stress that rocky shores and their tidepools support a rich community of these protists (Fig. 1).

PROTISTS TOO BIG TO PLACE BETWEEN A SLIDE AND A COVER GLASS

A few groups of protists (Granuloreticulosa, Ciliata, and Dinozoa) that are common in tidepools and the intertidal zone include organisms that cannot be compressed between ordinary microscope slides and cover glasses. These organisms should be examined in a good-quality dissecting microscope or, without cover glasses, under a low-power compound microscope.

Phylum Granuloreticulosa (Foraminifera)

Most members of this phylum (see Fig. 1N, O, R, S, T) are larger than 0.1 mm. Some of the largest found in tidepools reach >3 mm. Commonly called foraminifera, this group has anastomosing (spider web-like) granular pseudopods with bidirectional streaming. Most of the common ones build either calcareous tests (shells) or tests made by agglutinating particles. Agglutinated tests are easiest to detect in a dissection microscope when they are dry. Foraminifera with agglutinated tests are common in the littoral and supra-littoral zones and in the deep sea. Test composition (calcareous or agglutinated) is a major taxonomic criterion. Calcareous tests include those with or without pores. Most foraminifera are multichambered, adding chambers as they grow. The pattern of test growth is a character used to separate genera. Chambers can be added linearly to produce monoserial, biserial, or triserial tests, in a flat spiral, or in a raised spiral. Some grow to look like a coil or a paper clip. Location of apertures, places where the

pseudopods emerge from the test, and ornamentation are other important characters. Foraminifera are usually very patchy in their distribution in the field. As is true for many protists, their distribution may be restricted to particular zones, regions, or habitats. Two large (1–3 mm) foraminifera, *Amphistigina* and *Heterostegina*, which bear orange-brown symbionts, are common in Hawaiian tidepools and the shallow subtidal zones of many well-illuminated tropical and subtropical seas. Star sands (calcarinid foraminifera) are found in similar habitats in the Pacific.

<AUG1>

Phyla Ciliata and Dinozoa

Only a fraction of the members of these phyla found in tide pools and the littoral zone are too large to be examined in the compound microscope, so they will be treated in the next section.

PROTISTS EASILY IDENTIFIED USING A COMPOUND MICROSCOPE

Before the wide employment of electron-microscopic and molecular techniques, protists were identified by placing them in groups based on whether they were photosynthetic or not and whether they were motile or not. If they were motile, the type of motility (flagellated, amoeboid, ciliated, or gliding) became an important separating factor. The nature of the cell covering (tests, frustules, scales, pellicle) or internal skeletal elements (spines, axonemes) are also major factors separating groups of protists in tidepools and littoral zones. Following are the characteristics of some of the major groups of protists found in these habitats.

Phylum Bacillariophyta (Diatoms)

Diatoms (Fig. 1A, B, C, F, G) have exquisitely beautiful silica glass shells (frustules) that are best seen when the rest of the organism is digested away. They are extremely abundant primary producers in all aquatic habitats, including the ones of present interest, and are important food sources for many organisms. Diatoms may be round and radially symmetrical (Centrobacillariophyta) or elongate with a bilateral plane of symmetry (Pennatebacillariophyta). The frustule is made of two valves, which fit together like a Petri dish and its cover. The centric forms tend to dominate the plankton in the water column, while the pennate forms (some of which attach and others actively glide) are found in the benthos. Some of the centric diatoms are globelike, while others are flattened. Some of the most common genera of diatoms found in tidepools include *Cyclotella* (Fig. 1G), *Coccinodiscus*,

<AUG3>

Navicula, *Nitzschia* (Fig. 1B), *Amphora* (Fig. 1C), and *Synedra*. Other golden-pigmented (Chromista) photosynthetic protists with silica skeletons include the Prymnesiophyta and Silicoflagellata.

Phylum Dinozoa (Dinoflagellates), Also Known by Phycologists as Division Dinoflagellata

Dinoflagellates (Fig. 1P, Q, U) are very common in most aquatic environments and quite abundant in tidepools and the intertidal. Most dinoflagellates are photosynthetic and important in food webs. The nucleus of dinoflagellates is a unique feature of the group, because it contains chromosomes that are usually condensed during all phases of the cell cycle. Most dinoflagellates contain two flagella that are quite different in their structure. These produce a corkscrew-style locomotion. The flagella emerge from the ventral side of the cell. The flat ribbonlike flagellum, which causes the cell to rotate in its axis, wraps around the body in a groove known as a cingulum or girdle. The longitudinal flagellum lies in a groove (sulcus) that runs posteriorly from the flagellar pore to the posterior end of the cell. The position of the cingulum (anterior, central, posterior, or spiraling) is an important character used to separate genera of some groups. Dinoflagellates have a distinct theca, the structure of which is seen only by transmission electron microscopy (TEM). This complex cell covering, known as the amphiesma, consists of inner and outer membranes, between which lie a series of flattened vesicles. At the light microscopic level, it is possible to recognize thecal plates, which are formed in the vesicles of armored species. Dinoflagellate groups are separated from each other by whether they have recognizable plates (Gonyaulacales, Peridinales, Dinophysiales, Prorocentrales) or not (Syndales, Phytodinales, Noctilucales, Bastidinales, Desmocapsales, Suessiales, and Gymnodinales), and by the plate patterns of those dinoflagellates that have them. One might expect almost any of the >100 common genera to be found in the waters of tidepools and littoral zones. Species of the dinoflagellate *Amphidinium* (Fig. 1U) are found swimming between the sedimentary particles of all intertidal habitats and on the benthos of every tidepool. Other unarmored common genera are *Gymnodinium* and *Gyrodinium*. Most common among the armored genera that might be found are *Peridinium*, *Gonyaulax*, and *Dinophysis* (Fig. 1Q). Often a tidepool will have a reddish tinge caused by a bloom of dinoflagellates. Of additional note are the dinoflagellates often referred to as the zooxanthellae. These are the photosynthetic, mutualistic endosymbionts (e.g., of the genus *Symbiodinium*) found in certain rocky intertidal and subtidal sea anemones

(e.g., the aggregating anemone, *Anthopleura elegantissima*, Fig. 2, and the giant green anemone, *Anthopleura xanthogrammitica*), as well as within reef-building corals, certain marine sarcodines (e.g., Foraminifera and Radiolaria), flatworms, and the tropical Indo-Pacific giant clam *Tridacna*.

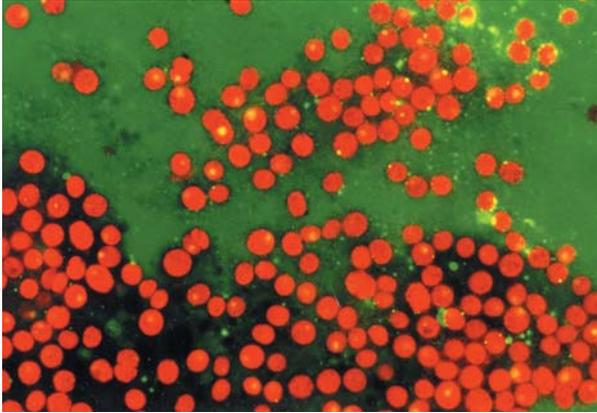


FIGURE 2 Epifluorescence micrograph (under blue light excitation) of *Symbiodinium*, a dinoflagellate endosymbiont extracted from the aggregating anemone *Anthopleura elegantissima*. Cells average about 10 μm in diameter. Image by.

<AUG2>

Phylum Ciliophora

Ciliates (Fig. 1D, E, H, I, M) are abundant in every aquatic habitat and in soils. All but a few have cilia on their surface at one time in their life cycle. Most have two kinds of nuclei; the larger one (or more) the macronucleus regulates metabolism; the smaller one (or more) is primarily involved in sexual recombination. Most ciliates are phagotrophic, ingesting nutrients through their cytostomes into a cytopharynx, which may be surrounded by specialized ciliary structures. The organization of the oral and somatic regions (the somatic region functions in locomotion, attachment, forming protective coverings, and sensing the environment) are the main characters used to subdivide the phylum into 10 classes. Identifying ciliates involves careful study of the distribution of cilia and associated fibrils. Ciliate specialists use a silver staining technique and TEM for identification. The nonspecialist can identify certain groups of common ciliates by some superficial observations, such as attachment to the sides or bottom of tide pools. One of the easiest groups to identify is the subclass Peritrichia. These may have long or short contractile stalks. Their cytostome is surrounded by a crown of prominent peristomal ciliation. Related to the peritrichs, the chonotrichs have noncontractile

bodies. Another common group of attached ciliates are the Suctoria. Adults lack cilia and a cytostome. They have tentacles that capture and digest prey. Some of the ciliates that crawl along surfaces are flattened and ribbon-like (class Litostomatea). Another group of crawling ciliates likely to be found in the littoral and every tidepool is the subclass Hypotrichia. These small, ovoid, dorsoventrally flattened ciliates have composite tufts of somatic cilia (cirri) that function as a single unit. The cirri occur in definite patterns on their ventral surfaces. Another group of ciliates, class Karyorelecta, order Protostomatida, resemble nematodes crawling and swimming on and in the benthos. Their cytostomes are anterior. Members of the class Oligohymenophorea are abundant in the water column. Some of them have a prominent velum (sail-like structure), which acts to funnel food into the cytostome. The proper identification of a large variety of other small ciliates requires more sophisticated methods.

SMALL FLAGELLATED GROUPS

There is a diversity of nonrelated, free-living small flagellates (Fig. 1J, L) that include marine representatives (e.g., class Choanoflagellata (colored flagellates), order Volvocida (biflagellated oval green flagellates), straminophiles (nonpigmented and orange- or red-pigmented flagellates with chlorophylls *a* and *c*; order Bicoecida, class Chrysoomonadida, class Pelagiophyceae, order Raphidomonadida, class Silicoflagellata), order Cryptomonadida, phylum Euglenozoa, class Pedinophyceae, order Prymnesiida, and some residual heterotrophic flagellates with too few representatives to be grouped above the family level. A few of these flagellates are easily recognized because of their unusual skeletons, a cleft in their anterior, or scales that are observable in the light microscope, but most require observation under TEM for definitive identification. Except for the very small (5 μm) flagellates, these groups are very rarely abundant in rocky-shore and tidepool habitats, most being brought in the wash of plankton in each tidal cycle. Some genera, such as *Dunaliella* (Volvocida), are always present in small numbers.

Naked Amoebae

Naked amoebae (Fig. 1K) are always present in tide pools and in littoral habitats. They are usually small, inconspicuous, and easily overlooked. Stellate forms of many genera can be found in the water column, but most of them crawl on vegetation, debris, or benthic substrate. To find them it is often better to place a sample in a covered aquarium or on a Petri plate with or without a non-nutrient agar. As soon as the surface is colonized by

bacteria and diatoms, the amoebae become abundant. Sometimes the explosive bursts of amoebae are dramatic, with a resultant dramatic clearing of a bacterial or diatom layer where the amoebae have eaten. Common amoebae found in tidepools can be recognized by their shape, possession of a uroid (posterior end, which may be bulbous, globular, papillate, etc.), the nature of their pseudopods (monopodal, polypodal, slender, radiating, etc.) and whether locomotion is smooth or eruptive. Some marine amoebae have scales or spicules, which are not always obvious to the untrained eye.

NUTRITION AND FOOD WEB INTERACTIONS

Marine organisms sustain themselves as autotrophs (strictly photosynthesis), mixotrophs (chemosynthesis or photosynthesis supplemented with other outside nutritional sources or symbioses), or heterotrophs (outside food sustained from some combination of absorption and ingestion). A plethora of algae sustaining themselves entirely or primarily by photosynthesis live both in the euphotic zone of the water column as well as in, on, or associated with shallow-water coastal marine sediments and seamounts. Which ones are to be found is determined by many physiochemical and biological factors. Key to this are sediment type and size (rocks to sand, muds, organic oozes) and living surfaces. Well represented in association with the sediments are diatoms, certain dinoflagellates, and small flagellates as well as other microalgae and seaweeds (Figs. 1 and 3).

In general, primarily heterotrophic protists gain nutrition from some combination of absorption of dissolved organic materials, photosynthesis, chemosynthesis, phagotrophy, or

symbiosis (including mutualism, commensalisms, and parasitism). Phagotrophy might involve bacteria, cyanobacteria, microalgae, other protists, and, for some (e.g., foraminiferan and radiolarian solitary and colonial amoeboids), even multicellular invertebrates and small vertebrates. For parasitic protists, large hosts often serve as a nutritional source.

Because of limitations imposed by the physics of diffusion relative to organism size and surface-area-to-volume ratios, dissolved organics as a sole source of nutrition are generally adequate only for bacteria. In turn, because of normal water column bacterial concentrations, physical hydrodynamic filtration limitations, and metabolic needs, planktobacteria cannot support the growth of most larger protists such as planktonic ciliates but do support small flagellate predators. Many of the flagellates also can eat other protists their own size and larger. The planktonic ciliates generally eat microalgae and other protists, including ciliates. Many of the water column amoeboid forms feed on larger prey, including various planktonic crustaceans and small fish, in addition to smaller food items. Surface-to-volume ratios increase with decreasing particle size. So, in the sediments, depending on particle sizes and associated surface-to-volume ratios, concentrations of organics are generally higher than in the water column. For that reason, in addition to bacterivorous flagellates in sediments, many of the ciliates found there are bacterivorous in nature, and thus taxonomically distinct from the water column ciliates. Many amoeboid forms are also found in the sediments feeding on a host of prey, including bacteria, cyanobacteria, diatoms and other algae, larger protists, and certain metazoans. Taxonomic variations follow the sediment size gradients as well as physiochemical and biological stresses.

SEE ALSO THE FOLLOWING ARTICLES

Collection and Preservation of Tidepool Organisms / Food Webs / Microbes / Micrometazoans / Nutrients

FURTHER READING

- Capriulo, G.M. ed. 1990. *Ecology of marine protozoa*. New York: Oxford University Press.
- Jahn, T. L., E. C. Bovee, and F. F. Jahn. 1979. *How to know the Protozoa*. Dubuque, IA: Wm. Brown Co..
- Knox, G. A. 2001. *The ecology of seashores*. Boca Raton, FL: CRC Press.
- Lee, J. J., G. F. Leedale, and P. Bradbury, eds. 2000. *An illustrated guide to the protozoa*, 2nd ed. Lawrence, KS: Society of Protozoologists/Allen Press..
- Lee, J. J., and A.T. Soldo. 1991. *Protocols in protozoology*. Lawrence, KS: Society of Protozoologists/Allen Press.
- Reid, P. C., C. M. Turley, and P. H. Burkill, eds. 1991. *Protozoa and their role in marine processes*. NATO ASI Series 25. Berlin: Springer-Verlag..
- Sieburth, J. M. 1979. *Sea microbes*. New York: Oxford University Press.

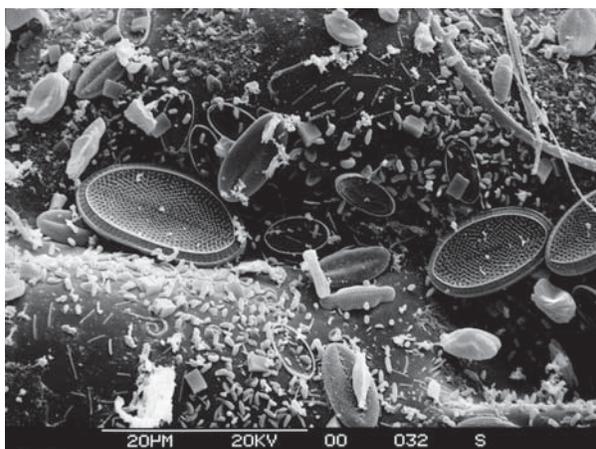


FIGURE 3 Scanning electron micrograph of a small tidepool rock surface showing colonization by bacteria and diatoms, some typical rocky-shore and tidepool food for grazing protists. Image by

<AUG2>