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MARINE BIOLOGY

COMPILED BY JOHN H. STEELE

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MARINE BIOLOGY

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This volume is a selection of articles from the second, electronic, edition of the *Encyclopedia of Ocean Science*. It is one of nine volumes that focus on particular aspects of marine studies. Marine Biology not only covers a great variety of plant and animal species but refers to diverse aspects of their physical, chemical and human environment.

The volume is divided into the traditional sub-disciplines: Plankton, Benthos, Fish, Marine Mammals and Seabirds. Within each category, there are articles on the main taxonomic groups, but also articles dealing with important processes such as primary production of phytoplankton, fish locomotion, feeding and foraging, marine mammal diving physiology and seabird conservation.

Marine organisms have an intimate relation with their fluid environment. Ocean currents play a large role in determining their migrations and vertical mixing and advection control the nutrient supply that regulates their food production. Longer term changes in these physical processes cause major stresses on populations and communities. This close coupling of ocean physics and biology is a theme of many articles, especially those concerned with the impact of climatic changes on plankton, marine mammals and seabirds.

There are others stresses on marine communities. The general topic of marine pollution is dealt with in a separate volume. The impact of fisheries not only on commercial stocks of fish but also on the remainder of their ecosystems, is considered at length in a companion volume to this one dealing broadly with ecological processes.

Each section of this volume opens with an “Overview” article written by the Section Editor responsible for this theme within the Encyclopedia. These Section Editors were also involved in the selection of authors for the individual topics. The Editors of the Encyclopedia are in their debt for their work in ensuring the quality and coverage of these articles.

Given the breadth of topics under the rubric of Marine Biology and their inter-relation with other aspects of ocean science, this one volume must be considered as a summary or introduction. For this reason each article has, not only a further reading list, but also references to articles in the Encyclopedia or in other volumes in this series.

The articles in this volume could not have been produced without the considerable help of the members of the Editorial Advisory Board of the Encyclopedia’s second edition, from which these articles were chosen. The board provided advice and suggestions about the content and authorship of particular subject areas covered in the Encyclopedia. In addition to thanking the authors of the articles in this volume, the Editors wish to thank the members of the Editorial Board for the time they gave to identify and encourage authors, to read and comment on (and sometimes to suggest improvements to) the written articles, and to make this venture possible.

John H. Steele
Editor

PLANKTON & NEKTON

PLANKTON OVERVIEW

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The category of marine life known as plankton represents the first step in the food web of the ocean (and of large bodies of fresh water), and components of the plankton are food for many of the fish harvested by humans and for the baleen whales. The plankton play a major role in cycling of chemical elements in the ocean, and thereby also affect the chemical composition of sea water and air (through exchange of gases between the sea and the overlying atmosphere). In the parts of the ocean where planktonic life is abundant, the mineral remains of members of the plankton are major contributors to deep-sea sediments, both affecting the chemistry of the sediments and providing a micropaleontological record of great value in reconstructing the earth's history.

'Plankton' refers to 'drifting', and describes organisms living in the water column (rather than on the bottom – the benthos) and too small and/or weak to move long distances independently of the ocean's currents. However, the distinction between plankton and nekton (powerfully swimming animals) can be difficult to make, and is often based more on the traditional method of sampling than on the organisms themselves.

Although horizontal movement of plankton at kilometer scales is passive, the metazoan zooplankton nearly all perform vertical migrations on scales of 10s to 100s of meters. This depth range can take them from the near surface lighted waters where the phytoplankton grow, to deeper, darker and usually colder environments. These migrations are generally diurnal, going deeper during the day, or seasonal, moving to deeper waters during the winter months to return to the surface around the time that phytoplankton production starts. The former pattern can serve various purposes: escaping visual predators and scanning the watercolumn for food. (It should be noted that predators such as pelagic fish also migrate diurnally.) Seasonal descent to greater depths is a common feature for several copepod species and may conserve energy at a time when food is scarce in the upper layers. However, vertical migration has another role. Because of differences in current strength and direction between surface and deeper layers in the ocean, time spent in deeper water acts as a transport mechanism relative to the near surface layers. On a daily basis this process can take plankton into different food concentrations. Seasonally, this effective 'migration' can complete a spatial life cycle.

The plankton can be subdivided along functional lines and in terms of size. The size category, picoplankton (0.2–2.0 μm), is approximately equivalent to the functional category, bacterioplankton; most phytoplankton (single-celled plants or colonies) and protozooplankton (single-celled animals) are nano- or microplankton (2.0–20 μm and 20–200 μm, respectively). The metazoan zooplankton (animals, the 'insects of the sea') includes large medusae and siphonophores several meters in length. Size is more important in oceanic than in terrestrial ecosystems because most of the plants are small (the floating seaweed, *Sargassum*, being the notable exception), predators generally ingest their prey whole (there is no hard surface on which to rest prey while dismembering it), and the early life stages of many types of zooplankton are approximately the same size as the larger types of phytoplankton. Therefore, while the dependence on light for photosynthesis is characteristic of the phytoplankton, the concepts of 'herbivore' and 'carnivore' can be ambiguous when applied to zooplankton, since potential plant and animal prey overlap in size and can be equivalent sources of food. Though rabbits do not eat baby foxes on land, analogous ontogenetic role-switching is very common in the plankton.

Among the animals, holoplanktonic species are those that spend their entire life in the plankton, whereas many benthic invertebrates have meroplanktonic larvae that are temporarily part of the plankton. Larval fish are also a temporary part of the plankton, becoming part of the nekton as they grow. There are also terms or prefixes indicating special habitats, such as 'neuston' to describe zooplanktonic species whose distribution is restricted to within a few centimeters of the sea's surface, or 'abyssoplankton' to describe animals living only in the deepest waters of the ocean. Groups of such species form communities (see below).

Since the phytoplankton depend on sunlight for photosynthesis, this category of plankton occurs almost entirely from the surface to 50–200 m of the ocean – the euphotic depth (where light intensity is 0.1–1% of full surface sunlight). Nutrients such as nitrate and phosphate are incorporated into protoplasm in company with photosynthesis, and returned to dissolved form by excretion or remineralization of dead organic matter (particulate detritus). Since much of the latter process occurs after sinking of the detritus, uptake of nutrients and their regeneration are partially separated vertically. Where and when photosynthesis is proceeding actively and vertical mixing is not excessive, a near-surface layer of low nutrient concentrations is separated from a layer of abundant nutrients, some distance below the euphotic depth, by a nutricline (a layer in which nutrient concentrations increase rapidly with depth). Therefore, the spatial and temporal relations between the euphotic depth (dependent on light intensity at the surface and the turbidity of the water), the nutricline, and the pycnocline (a layer in which density increases rapidly with depth) are important determinants of the abundance and productivity of phytoplankton.

Zooplankton is typically more concentrated within the euphotic zone than in deeper waters, but because of sinking of detritus and diel vertical migration of some species into and out of the euphotic zone, organic matter is supplied and various types of zooplankton (and bacterioplankton and nekton) can be found at all depths in the ocean. An exception is anoxic zones such as the deep waters of the Black Sea, although certainly types of bacterioplankton that use molecules other than oxygen for their metabolism are in fact concentrated there.

Even though the distributions of planktonic species are dependent on currents, species are not uniformly distributed throughout the ocean. Species tend to be confined to particular large water masses, because of physiological constraints and inimical interactions with other species. Groups of species, from small invertebrates to active tuna, seem to 'recognize' the same boundaries in the oceans, in the sense that their patterns of distribution are similar. Such groups are called 'assemblages' (when emphasizing their statistical reality, occurring together more than expected by chance) or 'communities' (when emphasizing the functional relations between the members in food webs), though terms such as 'biocoenoses' can be found in older literature. Thus, one can identify 'central water mass,' 'subantarctic,' 'equatorial,' and 'boreal' assemblages associated with water masses defined by temperature and salinity; 'neritic' (i.e. nearshore) versus 'oceanic' assemblages with respect to depth of water over which they occur, and 'neustonic' (i.e. air–sea interface), 'epipelagic,' 'mesopelagic,' 'bathypelagic,' and 'abyssopelagic' for assemblages distinguished by the depth at which they occur. Within many of these there may be seasonally distinguishable assemblages of organisms, especially those with life spans of less than one year.

Regions which are boundaries between assemblages are sometimes called ecotones or transition zones; they generally contain a mixture of species from both sides, and (as in the transition zone between subpolar and central water mass assemblages) may also have an assemblage of species that occur only in the transition region.

Despite the statistical association between assemblages and water masses or depth zones, it is far from clear that the factor that actually limits distribution is the temperature/salinity or depth that physically defines the water mass or zone. It is likely that a few important species have physiological limits confining them to a zone, and the other members of the assemblage are somehow linked to those species functionally, rather than being themselves physiologically constrained. Limits can be imposed on certain life stage, such as the epipelagic larvae of meso- or bathypelagic species, creating patterns that reflect the environment of the sensitive life stage rather than the adult. Conversely, meroplanktonic larvae, such as the phyllosome of spiny lobsters, can often be found far away from the shallow waters that are a suitable habitat for the adults.

See also

Bacterioplankton. Gelatinous Zooplankton. Protozoa, Planktonic Foraminifera.

Further Reading

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MARINE PLANKTON COMMUNITIES

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Introduction

By definition, a community is an interacting population of various kinds of individuals (species) in a common location (*Webster's Collegiate Dictionary*, 1977).

The objective of this article is to provide general information on the composition and functioning of various marine plankton communities, which is accompanied by some characteristic details on their dynamicism.

General Features of a Plankton Community

The expression 'plankton community' implies that such a community is located in a water column. It has a range of components (groups of organisms) that can be organized according to their size. They range in size from tiny single-celled organisms such as bacteria (0.4–1-μm diameter) to large predators like scyphomedusae of more than 1 m in diameter. A common method which has been in use for decades is to group according to size, which here is attributed to the organism's largest dimension; thus the organisms range from picoplankton to macroplankton (**Figure 1**). It is, however, the smallest dimension of an organism which usually determines whether it is retained by a mesh, since in a flow, elongated particles align themselves with the flow.

A plankton community is operating/functioning continuously, that is, physical, chemical, and biological variables are always at work. Interactions among its components occur all the time. As one well-known fluid dynamicist stated, "The surface of the ocean can be flat calm but below that surface there is always motion of the water at various scales." Many of the particles/organisms are moving or being moved most of the time: Those without flagella or appendages can do so due to processes within or due to external forcing, for example, from water motion due to internal waves; and those with flagella/cilia or appendages or muscles move or create motion of the water in order to exist. Oriented motion is usually in the vertical which often results in distinct layers of certain organisms. However, physical variables also, such as light or density differences of water masses, can result in layering of planktonic organisms. Such layers which are often horizontally extended are usually referred to as patches.

As stated in the definition, the components of a plankton community interact. It is usually the case that a larger organism will ingest a smaller one or a part of it (**Figure 1**). However, there are exceptions. The driving force for a planktonic community originates from sun energy, that is, primary productivity's (1) direct and (2) indirect products: (1) autotrophs (phytoplankton cells) which can range from near 2 to more than 300-μm width/diameter, or chemotrophs; and (2) dissolved organic matter, most of which is released by phytoplankton cells and protozoa as metabolic end products, and being taken up by bacteria and mixo- and heterotroph protozoa (**Figure 1**). These two components mainly set the microbial loop (ML; (*see* Bacterioplankton and Protozoa, Planktonic Foraminifera)) in motion; that is, unicellular organisms of different sizes and behaviors (auto-, mixo-, and heterotrophs) depend on each other – usually, but not always, the smaller being ingested by the larger. Most of nutrients and energy are recirculated within this subcommunity of unicellular organisms in all marine regions of our planet (*see* Bacterioplankton, Phytoplankton Size Structure, and Protozoa, Planktonic Foraminifera for more details, especially the ML)These processes of the ML dominate the transfer of energy in all plankton communities largely because the processes (rates of ingestion, growth, reproduction) of unicellular heterotrophs almost always outpace those of phytoplankton, and also of metazooplankton taxa at most times.

The main question actually could be: "What is the composition of plankton communities, and how do they function?" **Figure 1** reveals sizes and relationships within a plankton community including the ML. It shows the so-called 'bottom-up' and 'top-down' effects as well as indirect effects like the above-mentioned labile dissolved organic matter (labile DOM), released by auto- and also by heterotrophs, which not only drives bacterial growth but can also be taken up or used by other protozoa. There can also be reversals, called two-way processes. At times a predator eating an adult metazoan will be affected by the same metazoan which is able to eat the predator's early juveniles (e.g., well-grown ctenophores capturing adult omnivorous copepods which have the ability to capture and ingest very young ctenophores).

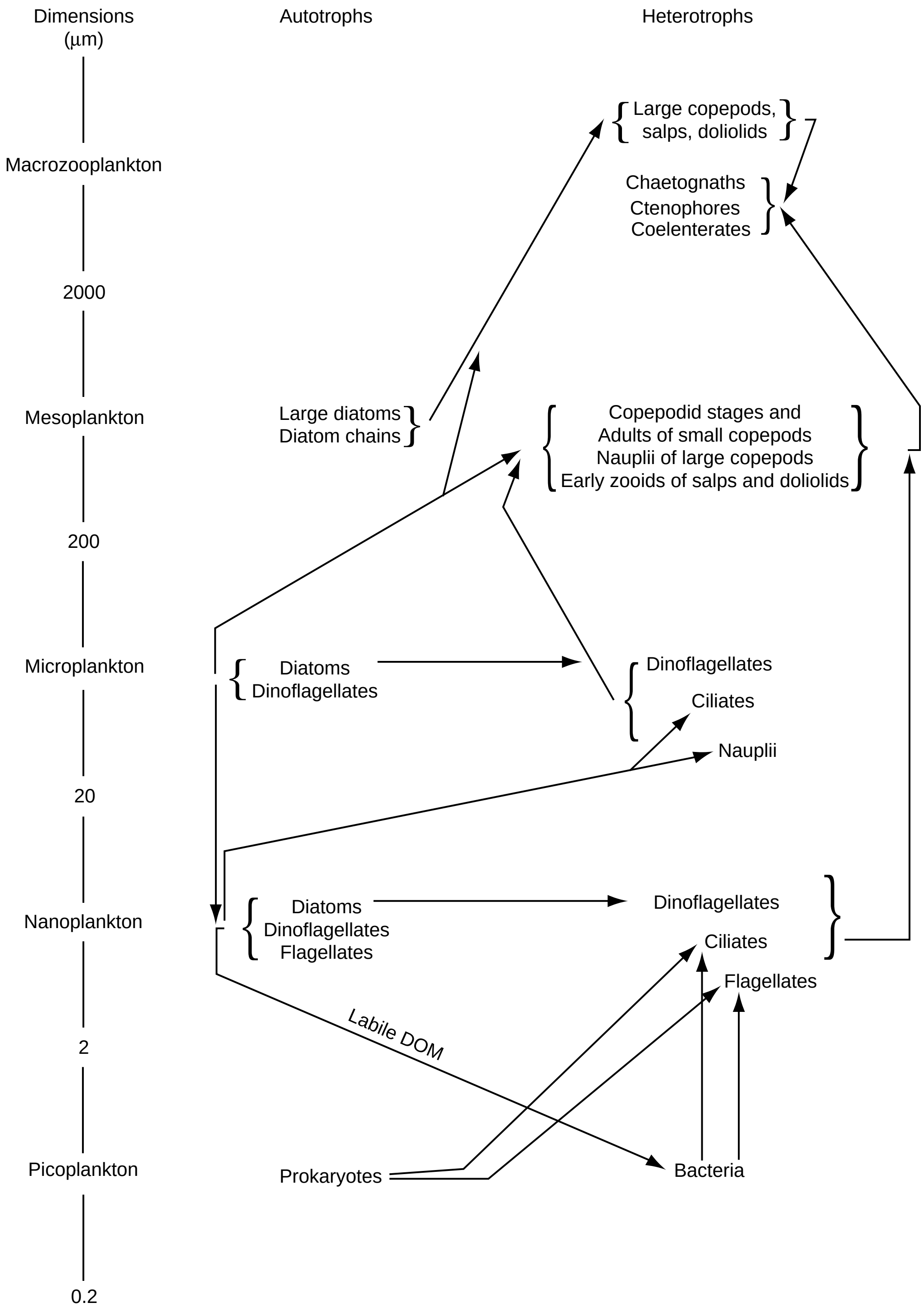

Figure 1 Interactions within a plankton community separated into size classes of auto- and heterotrophs, including the microbial loop; the arrows point to the respective grazer, or receiver of DOM; the figure is partly related to figure 9 from Landry MR and Kirchman DL (2002) Microbial community structure and variability in the tropical Pacific. *Deep-Sea Research II* 49: 2669–2693.

To comprehend the functioning of a plankton community requires a quantitative assessment of the abundances and activities of its components. First, almost all of our knowledge to date stems from *in situ* sampling, that is, making spot measurements of the abundance and distribution of organisms in the water column. The accurate determination of abundance and distribution requires using meshes or devices which quantitatively collect the respective organisms. Because of methodological difficulties and insufficient comprehension of organisms' sizes and activities, quantitative sampling/quantification of a community's main components has been often inadequate. The following serves as an example of this. Despite our knowledge that copepods consist of 11 juvenile stages aside of adults, the majority of studies of marine zooplankton hardly considered the juveniles' significance and this manifested itself in sampling with meshes which often collected merely the adults quantitatively. Second, much knowledge on rate processes comes from quantifying the respective organisms' activities under controlled conditions in the laboratory. Some *in situ* measurements (e.g., of temperature, salinity, chlorophyll concentrations, and acoustic recordings of zooplankton sizes) have been achieved 'continuously' over time, resulting in time series of increases and decreases of certain major community components. To date there are few, if any, direct *in situ* observations on the activity scales of the respective organisms, from bacteria to proto- and to metazooplankton, mainly because of methodological difficulties. In essence, our present understanding of processes within plankton communities is incomplete.

Specific Plankton Communities

We will provide several examples of plankton communities of our oceans. They will include information about the main variables affecting them, their main components, partly their functioning over time, including particular specifics characterizing each of those communities.

In this section, plankton communities are presented for three different types of marine environments: estuaries/inshore, continental shelves, and open ocean regions.

Estuaries

Estuaries and near-shore regions, being shallow, will rapidly take up and lose heat, that is, will be strongly affected by atmospheric changes in temperature, both short- and long-term, the latter showing in the seasonal extremes ranging from 2 to 32 °C in estuaries of North Carolina. Runoff of fresh water, providing continuous nutrient input for primary production, and tides contribute to rapid changes in salinity. This implies that resident planktonic taxa ought to be eurytherm as well as – therm. Only very few metazooplanktonic species are able to exist in such an environment (**Table 1**). In North Carolinian estuaries, representative of other estuaries, they are the copepod species *Acartia tonsa*, *Oithona oculata*, and *Parvocalanus crassirostris*. In estuaries of Rhode Island, two species of the genus *Acartia* occur. During colder temperatures *Acartia hudsonica* produces dormant eggs as temperatures increase and then is replaced by *A. tonsa*, which produces dormant eggs once temperatures again decrease later in the year. Such estuaries are known for high primary productivity, which is accompanied by high abundances of heterotroph protozoa preying on phytoplankton. Such high abundances of unicellular organisms imply that food is hardly limiting the growth of the above-mentioned copepods which can graze on auto- as well as heterotrophs. However, such estuaries are often nursery grounds for juvenile fish like menhaden which prey heavily on late juveniles and adults of such copepods, especially *Acartia*, which is not only the largest of those three dominant copepod species but also moves the most, and thus can be seen most easily by those visual predators. This has resulted in diurnal migrations mostly of their adults, remaining at the seafloor during the day where they hardly eat, thus avoiding predation by such visual predators, and only entering the water column during dark hours. That then is their period of pronounced feeding. The other two species which are not heavily preyed upon by juvenile fish, however, can be affected by the co-occurring *Acartia*, because from early copepodid stages on this genus can be strongly carnivorous, readily preying on the nauplii of its own and of those other species.

Nevertheless, the usually continuous abundance of food organisms for all stages of the three copepod species results in high concentrations of nauplii which in North Carolinian estuaries can reach $100\,\mathrm{l}^{-1}$, as can their combined copepodid stages. The former is an underestimate, because sampling was done with a 75-µm mesh, which is passed through by most of those nauplii. By comparison, in an estuary on the west coast of Japan (Yellow Sea), dominated also by the genera *Acartia*, *Oithona*, and *Paracalanus* and sampling with 25-µm mesh, nauplius concentrations during summer surpassed $700\,\mathrm{l}^{-1}$, mostly from the genus *Oithona*. And copepodid stages plus adults repeatedly exceeded $100\,\mathrm{l}^{-1}$. Here sampling with such narrow mesh ensured that even the smallest copepods were collected quantitatively.

In essence, estuaries are known to attain among the highest concentrations of proto- and metazooplankton. The known copepod species occur during most of the year, and are observed year after year which implies persistence of those species beyond decades.

Table 1 Some characteristics of marine plankton communities

	Estuaries	*Shelves*	*Open ocean gyres*		
			Subarctic Pacific	*Boreal Atlantic*	*Epipelagic subtropical*
					Atlantic/Pacific
Physical variables	Wide range of temperature and salinity	Intermittent and seasonal atmospheric forcing	Steady salinity, seasonal temp. variability	Major seasonal variability of temperature	Steady temperature and salinity, continuous atmospheric forcing
Nutrient supply	Continuous	Episodic	Seasonal	Seasonal	Occasional
Phytoplankton abundance	High from spring to autumn	Intermittently high	Always low	Major spring bloom	Always low
Phytoplankton composition	Flagellates, diatoms	Flagellates, diatoms, dinoflagellates	Nanoflagellates	Spring: diatoms Other: mostly nanoplankton	Mostly prokaryotes, small nano- and dinoflagellates
Primary Productivity	High at most times	Intermittently high	Maximum in spring	Max. in spring and autumn	Always low
No. of metazoan species	≤ 5	$\sim$10–30	>10	>20	>100
Seasonal variability of metazoan abundance	High spring and summer, low winter	Highly variable	High	High	Low
Copepod Ranges	N[a] $\sim$ 10–500 l^{-1}	$<$5–50 l^{-1}			3–10 l^{-1}
Abundance	Cop[b] $\sim$ 5–100 l^{-1}	$<$3–30 l^{-1}	Up to 1000 m^{-3}	Up to 1000 m^{-3}	300–1000 m^{-3}
			Neocalanus	*C. finmarchicus*	
Dominant metazooplankton taxa	*Acartia* *Oithona* *Parvocalanus*	*Oithona* *Paracalanus* *Temora* *Doliolida*	*Neocalanus* *Oithona* *Metridia*	*Calanus* *Oithona* *Oncaea*	*Oithona* *Clausocalanus* *Oncaea*

[a] Nauplii.

[b] Copepodids and adult copepods.

Continental Shelves

By definition they extend to the 200-m isobath, and range from narrow (few kilometers) to wide (more than 100-km width). The latter are of interest because the former are affected almost continuously and entirely by the nearby open ocean. Shelves are affected by freshwater runoff and seasonally changing physical variables. Water masses on continental shelves are evaluated concerning their residence time, because atmospheric events sustained for more than 1 week can replace most of the water residing on a wide shelf with water offshore but less so from near shore. This implies that plankton communities on wide continental shelves, which are often near boundary currents, usually persist for limited periods of time, from weeks to months (**Table 1**). They include shelves like the Agulhas Bank, the Campeche Banks/Yucatan Shelf, the East China Sea Shelf, the East Australian Shelf, and the US southeastern continental shelf. There can be a continuous influx year-round of new water from adjacent boundary currents as seen for the Yucatan Peninsula and Cape Canaveral (Florida). The momentum of the boundary current (here the Yucatan Current and Florida Current) passing a protruding cape will partly displace water along downstream-positioned diverging isobaths while the majority will follow the current's general direction. This implies that upstream-produced plankton organisms can serve as seed populations toward developing a plankton community on such wide continental shelves.

Whereas estuarine plankton communities receive almost continuously nutrients for primary production from runoff and pronounced benthic-pelagic coupling, those on wide continental shelves infrequently receive new nutrients. Thus they are at most times a heterotroph community unless they obtain nutrients from the benthos due to storms, or receive episodically input of cool, nutrient-rich water from greater depths of the nearby boundary current as can be seen for the US SE shelf. Passing along the outer shelf at about weekly intervals are nutrient-rich cold-core Gulf Stream eddies which contain plankton organisms from the highly productive Gulf of Mexico. Surface winds, displacing shelf surface water offshore, lead to an advance of the deep cool water onto the shelf which can be flooded entirely by it. Pronounced irradiance and high-nutrient loads in such upwellings result in phytoplankton blooms which then serve as a food source for protozoo- and metazooplankton. Bacteria concentrations in such cool water masses increase within several days by 1 order of magnitude. Within 2–3 weeks most of the smaller phytoplankton (*c.* <20-μm width) has been greatly reduced, usually due to grazing by protozoa and relatively slow-growing assemblages of planktonic copepods of various genera such as *Temora*, *Oithona*, *Paracalanus*, *Eucalanus*, and *Oncaea*. However, quite frequently, the Florida Current which becomes the Gulf Stream carries small numbers of Thaliacea (Tunicata), which are known for intermittent and very fast asexual reproduction. Such salps and doliolids, due to their high reproductive and growth rate, can colonize large water masses, the latter increasing from ~ 5 to >500 zooids per cubic meter within 2 weeks, and thus form huge patches, covering several thousands of square kilometers, as the cool bottom water is displaced over much of the shelf. The increased abundance of salps (usually in the warmer and particle-poor surface waters) and doliolids (mainly in the deeper, cooler, particle-rich waters, also observed on the outer East China shelf) can control phytoplankton growth once they achieve bloom concentrations. The development of such large and dense patches is partly due to the lack of predators.

Although the mixing processes between the initially quite cool intruding bottom (13–20 °C) and the warm, upper mixed layer water (27–28 °C) are limited, interactions across the thermocline occur, thus creating a plankton community throughout the water column of previously resident and newly arriving components. The warm upper mixed layer often has an extraordinary abundance of early copepodid stages of the poecilostomatoid copepod *Oncaea*, thanks to their ontogenetical migration after having been released by the adult females which occur exclusively in the cold intruding water. Also, early stages of the copepod *Temora turbinata* are abundant in the warm upper mixed layer; while *T. turbinata*'s late juvenile stages prefer the cool layer because of the abundance of large, readily available phytoplankton cells. As in estuaries, the copepod genus *Oithona* flourishes on warm, temperate, and polar continental shelves throughout most of the euphotic zone.

Such wide subtropical shelves will usually be well mixed during the cooler seasons, and then harbor, due to lower temperatures, fewer metazoplankton species which are often those tolerant of wider or lower temperature ranges. Such wide shelves are usually found in subtropical regions, which explains the rapidity of the development of their plankton communities. They, however, are also found in cooler climates, like the wide and productive Argentinian/Brazilian continental shelf about which our knowledge is limited. Other large shelves, like the southern North Sea, have a limited exchange of water with the open ocean but at the same time considerable influx of runoff, plus nutrient supply from the benthos due to storm events, and thus can maintain identical plankton communities over months and seasons.

In essence, continental shelf plankton communities are usually relatively short-lived, which is largely due to their water's limited residence time.

Open Ocean

The open ocean, even when not including ocean margins (up to 1000-m water column), includes by far the largest regions of the marine environment. Its deep-water columns range from the polar seas to the Tropics. All these regions are under different atmospheric and seasonal regimes, which affect plankton communities. Most of these communities are seasonally driven and have evolved along the physical conditions characterizing each region. The focus here is on gyres as they represent specific ocean communities whose physical environment can be readily presented.

Gyres represent huge water masses extending horizontally over hundreds to even thousands of kilometers in which the water moves cyclonically or anticyclonically. They are encountered in subpolar, temperate, and subtropical regions. The best-studied ones are:

- subpolar: Alaskan Gyre;
- temperate: Norwegian Sea Gyre, Labrador–Irminger Sea Gyre;
- subtropical: North Pacific Central Gyre (NPCG), North Atlantic Subtropical Gyre (NASG).

The Alaskan Gyre is part of the subarctic Pacific (**Table 1**) and is characterized physically by a shallow halocline (~110-m depth) which prevents convective mixing during storms. Biologically it is characterized by a persistent low-standing stock of phytoplankton despite high nutrient abundance, and several species of large copepods which have evolved to persist via a life cycle as shown for *Neocalanus plumchrus*. By midsummer, fifth copepodids (C5) in the upper 100 m which have accumulated large amounts of lipids begin to descend to greater depths of 250 m and beyond undergoing diapause, and eventually molt to females which soon begin to spawn. Spawning females are found in abundance from August to January. Nauplii living off their lipid reserves and moving upward begin to reach surface waters by mid- to late winter as copepodid stage 1 (C1), and start feeding on the abundant small phytoplankton cells (probably passively by using their second maxillae, but mostly by feeding actively on heterotrophic protozoa which are the main consumers of the tiny phytoplankton cells). The developing copepodid stages accumulate lipids which in C5 can amount to as much as 50% of their body mass, which then serve as the energy source for metabolism of the females at depth, ovary development, and the nauplii's metabolism plus growth. While the genus *Neocalanus* over much of the year provides the highest amount of zooplankton biomass, the cyclopoid *Oithona* is the most abundant metazooplankter; other abundant metazooplankton taxa include *Euphausia pacifica*, and in the latter part of the year *Metridia pacifica* and *Calanus pacificus*.

In the temperate Atlantic (**Table 1**), the Norwegian Sea Gyre maintains a planktonic community which is characterized, like much of the temperate oceanic North Atlantic, by the following physical features. Pronounced winds during winter mix the water column to beyond 400-m depth, being followed by lesser winds and surface warming resulting in stratification and a spring bloom of mostly diatoms, and a weak autumn phytoplankton bloom. A major consumer of this phytoplankton bloom and characteristic of this environment is the copepod *Calanus finmarchicus*, occurring all over the cool North Atlantic. This species takes advantage of the pronounced spring bloom after emerging from diapause at $>$400-m depth, by moulting to adult, and grazing of females at high clearance rates on the diatoms, right away starting to reproduce and releasing up to more than 2000 fertilized eggs during their lifetime. Its nauplii start to feed as nauplius stage 3 (N3), being able to ingest diatoms of similar size as the adult females, and can reach copepodid stage 5 (C5) within about 7 weeks in the Norwegian Sea, accumulating during that period large amounts of lipids (wax ester) which serve as the main energy source for the overwintering diapause period. Part of the success of *C. finmarchicus* is found in its ability of being omnivorous. C5s either descend to greater depths and begin an extended diapause period, or could moult to adult females, thus producing another generation which then initiates diapause at mostly C5. Its early to late copepodid stages constitute the main food for juvenile herring which accumulate the copepods' lipids for subsequent overwintering and reproduction. Of the other copepods, the genus *Oithona* together with the poecilostomatoid *Oncaea* and the calanoid *Pseudocalanus* were the most abundant.

Subtropical and tropical parts of the oceans cover more than 50% of our oceans. Of these, the NPCG, positioned between *c.* 10° and 45° N and moving anticyclonically, has been frequently studied. It includes a southern and northern component, the latter being affected by the Kuroshio and westerly winds, the former by the North Equatorial Current and the trade winds. Despite this, the NPCG has been considered as an ecosystem as well as a huge plankton community. The NASG, found between *c*. 15° and 40° N and moving anticyclonically, is of similar horizontal dimensions. There are close relations between subtropical and tropical communities; for example, the Atlantic south of Bermuda is considered close to tropical conditions. Vertical mixing in both gyres is limited. Here we focus on the epipelagic community which ranges from the surface to about 150-m depth, that is, the euphotic zone. The epipelagial is physically characterized by an upper mixed layer of *c*. 15–40 m of higher temperature, below which a thermocline with steadily decreasing temperatures extends to below 150-m depth. In these two gyres, the concentrations of phytoplankton hardly change throughout the year in the epipelagic (**Table 1**) and together with the heterotrophic protozoa provide a low and quite steady food concentration (**Table 1**) for higher trophic levels. Such very low particle abundances imply that almost all metazooplankton taxa depending on them are living on the edge, that is, are severely food-limited. Despite this fact, there are more than 100 copepod species registered in the epipelagial of each of the two gyres. How can that be? Almost all these copepod species are small and rather diverse in their behavior: the four most abundant genera have different strategies to obtain food particles: the intermittently moving *Oithona* is found in the entire epipelagial and depends on moving food particles (hydrodynamic signals); *Clausocalanus* is mainly found in the upper 50 m of the epipelagial and always moves at high speed, thus encountering numerous food particles, mainly via chemosensory; *Oncaea* copepodids and females occur in the lower part of the epipelagial and feed on aggregates; and the feeding-current producing *Calocalanus* perceives particles via chemosensory. This implies that any copepod species can persist in these gyres as long as it obtains sufficient food for growth and reproduction. This is possible because protozooplankton always controls the abundance of available food particles; thus, there is no competition for food among the metazooplankton. In addition, since total copepod abundance (quantitatively collected with a 63-μm mesh by three different teams) is steady and usually $<1000\,\mathrm{m}^{-3}$ including copepodid stages (pronounced patchiness of metazooplankton has not yet been observed in these oligotrophic waters), the probability of encounter (only a minority of the zooplankton is carnivorous on metazooplankton) is very low, and therefore the probability of predation low within the metazooplankton. In summary, these steady conditions make it possible that in the epipelagial more than 100 copepod species can coexist, and are in a steady state throughout much of the year.

Conclusions

All epipelagic marine plankton communities are at most times directly or indirectly controlled or affected by the activity of the ML, that is, unicellular organisms. Most of the main metazooplankton species are adapted to the physical and biological conditions of the respective community, be it polar, subpolar, temperate, subtropical, or tropical. The only metazooplankton genus found in all communities mentioned above, and also all other studied marine plankton communities, is the copepod genus *Oithona*. This copepod has the ability to persist under adverse conditions, for example, as shown for the subarctic Pacific. This genus can withstand the physical as well as biological (predation) pressures of an estuary, the persistent very low food levels in the warm open ocean, and the varying conditions of the Antarctic Ocean. Large copepods like the genus *Neocalanus* in the subarctic Pacific, and *C. finmarchicus* in the temperate to subarctic North Atlantic are adapted with respective distinct annual cycles in their respective communities. Among the abundant components of most marine plankton communities from near shore to the open ocean are appendicularia (Tunicata) and the predatory chaetognaths.

Our present knowledge of the composition and functioning of marine planktonic communities derives from (1) oceanographic sampling and time series, optimally accompanied by the quantification of physical and chemical variables; and (2) laboratory/onboard experimental observations, including some time series which provide results on small-scale interactions (microns to meters; milliseconds to hours) among components of the community. Optimally, direct *in situ* observations on small scales in conjunction with respective modeling would provide insights in the true functioning of a plankton community which operates continuously on scales of milliseconds and larger.

Our future efforts are aimed at developing instrumentation to quantify *in situ* interactions of the various components of marine plankton communities. Together with traditional oceanographic methods we would go ‘from small scales to the big picture’, implying the necessity of understanding the functioning on the individual scale for a comprehensive understanding as to how communities operate.

See also

Bacterioplankton. Copepods. Gelatinous Zooplankton. Phytoplankton Size Structure. Plankton Overview. Protozoa, Planktonic Foraminifera.

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PLANKTON VIRUSES

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Introduction

Although they are the tiniest biological entities in the sea, typically 20–200 nm in diameter, viruses are integral components of marine planktonic systems. They are extremely abundant in the water column, typically 10^{10} per liter in the euphotic zone, and they play several roles in system function: (1) they are important agents in the mortality of prokaryotes and eukaryotes; (2) they act as catalysts of nutrient regeneration and recycling, through this mortality of host organisms; (3) because of their host specificity and density dependence, they tend to selectively attack the most abundant potential hosts, thus may 'kill the winner' of competition and thereby foster diversity; and (4) they may also act as agents in the exchange of genetic material between organisms, a critical factor in evolution and also in relation to the spread of human-engineered genes. Although these processes are only now becoming understood in any detail, there is little doubt that viruses are significant players in aquatic and marine plankton.

History

It has only been in the past 25 years that microorganisms like bacteria and small protists have been considered 'major players' in planktonic food webs. The initial critical discovery, during the mid-1970s, was of high bacterial abundance as learned by epifluorescence microscopy of stained cells, with counts typically $10^9\,\mathrm{l}^{-1}$ in the plankton. These bacteria were thought to be heterotrophs (organisms that consume preformed organic carbon), because they apparently lacked photosynthetic pigments like chlorophyll (later it was learned that this was only partly right, as many in warm waters are in fact chlorophyll-containing prochlorophytes). With such high abundance, it became important to learn how fast they were dividing, in order to quantify their function in the food web. Growth rates were estimated primarily by the development and application of methods measuring bacterial DNA synthesis. The results of these studies showed that bacterial doubling times in typical coastal waters are about 1 day. When this doubling time was applied to the high abundance, to calculate how much carbon the bacteria are taking up each day, it became apparent that bacteria are consuming a significant amount of dissolved organic matter, typically at a carbon uptake rate equivalent to about half the total primary production. However, the bacterial abundance remains relatively constant over the long term, and they are too small to sink out of the water column. Therefore, there must be mechanisms within the water to remove bacteria at rates similar to the bacterial production rate. In the initial analysis, most scientists thought that grazing by protists was the only significant mechanism keeping the bacterial abundance in check. This was because heterotrophic protists that can eat bacteria are extremely common, and laboratory experiments suggested they are able to control bacteria at near-natural-abundance levels. However, some results pointed to the possibility that protists are not the only things controlling bacteria. In the late 1980s, careful review of multiple studies showed that grazing by protists was often not enough to balance bacterial production, and this pointed to the existence of additional loss processes. About that same time, data began to accumulate that viruses may also be important as a mechanism of removing bacteria. The evidence is now fairly clear that this is the case, and it will be outlined below. This article briefly summarizes much of what is known about how viruses interact with marine microorganisms, including general properties, abundance, distribution, infection of bacteria, mortality rate comparisons with protists, biogeochemical effects, effects on species compositions, and roles in genetic transfer and evolution.

General Properties

Viruses are small particles, usually about 20–200 nm long, and consist of genetic material (DNA or RNA, single or double stranded) surrounded by a protein coat (some have lipid as well). They have no metabolism of their own and function only via the cellular machinery of a host organism. As far as is known, all cellular organisms appear to be susceptible to infection by some kind of virus. Culture studies show that a given type of virus usually has a restricted host range, most often a single species or genus, although some viruses infect only certain subspecies and <0.5% may infect more than one genus. Viruses have no motility of their own, and contact the host cell by diffusion. They attach to the host usually via some normally exposed cellular component, such as a transport protein or flagellum. There are three basic kinds of virus reproduction (**Figure 1**). In lytic infection, the virus attaches to a host cell and injects its nucleic acid. This nucleic acid (sometimes accompanied by proteins carried by the virus) causes the host to produce numerous progeny viruses, the cell then bursts, progeny are released, and the cycle begins again. In chronic infection, the progeny virus release is not lethal and the host cell releases the viruses by extrusion or budding over many generations. In lysogeny after injection, the viral genome becomes part of the genome of the host cell and reproduces as genetic material in the host cell line unless an 'induction' event causes a switch to lytic infection. Induction is typically caused by DNA damage, such as from ultraviolet (UV) light or chemical mutagens such as mitomycin C. Viruses may also be involved in killing cells by mechanisms that do not result in virus reproduction.

Observation of Marine Viruses

Viruses are so small that they are at or below the resolution limit of light microscopy (*c.* 0.1 μm). Therefore electron microscopy is the only way to observe any detail of viruses. Sample preparation requires concentrating the viruses from the water onto an electron microscopy grid (coated with a thin transparent organic film). Because viruses are denser than seawater, this can be done by ultracentrifugation, typically at forces of at least 100 000 × g for a few hours. It should be noted that under ordinary gravity, forces like drag and Brownian motion prevent viruses from sinking. To be observable the viruses must be made electron-dense, typically by staining with uranium salts. The viruses are recognized by their size, shape, and staining properties (usually electron-dense hexagons or ovals, sometimes with a tail), and counted. Typical counts are on the order of 10^{10} viruses per liter in surface waters, with abundance patterns similar to those of heterotrophic bacteria (see below). Recently, it has been found that viruses can also be stained with nucleic acid stains like SYBR Green I, and observed and counted by

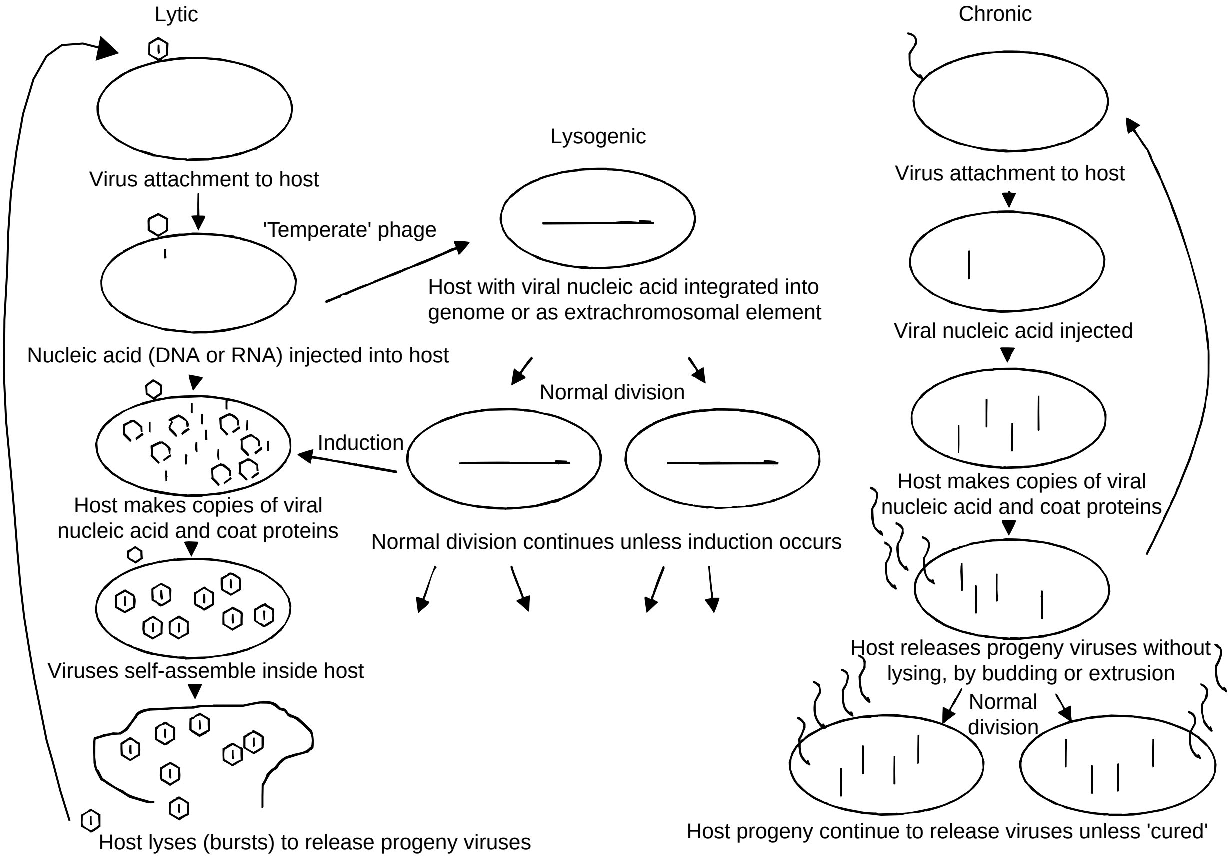

Figure 1 Virus life cycles. See text for explanation.

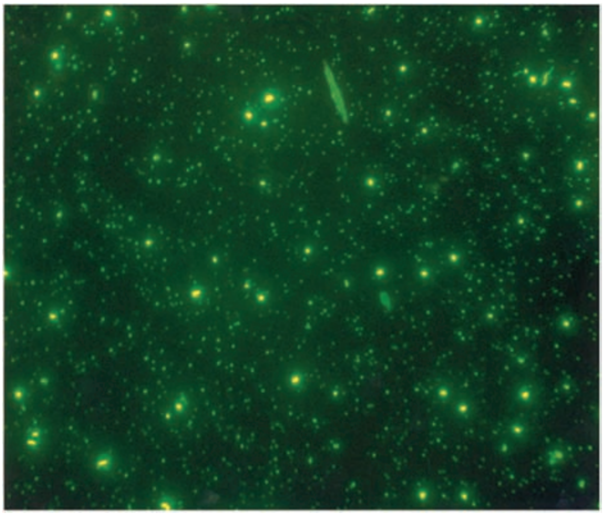

Figure 2 Epifluorescence micrograph of prokaryotes and viruses from 16 km offshore of Los Angeles, stained with SYBR Green I. The viruses are the very numerous tiny bright particles, and the bacteria are the rarer larger particles. Bacterial size is approximately 0.4–1 μm in diameter.

epifluorescence microscopy. This is faster, easier, and less expensive than transmission electron microscopy (TEM). Epifluorescence viewing of viruses is shown in **Figure 2**, a micrograph of SYBR Green I-stained bacteria and viruses, which dramatically illustrates the high relative virus abundance. Epifluorescence microscopy of viruses is possible even though the viruses are below the resolution limit of light because the stained viruses are a source of light and appear as bright spots against a dark background (like stars visible at night). Epifluorescence counts are similar to or even slightly higher than TEM counts from seawater.

What Kinds of Viruses Occur in Plankton?

Microscopic observation shows the total, recognizable, virus community, but what kinds of viruses make up this community, and what organisms are they infecting? Most of the total virus community is thought to be made up of bacteriophages (viruses that infect bacteria). This is because viruses lack metabolism and have no means of actively moving from host to host (they depend on random diffusion), so the most common viruses would be expected to infect the most common organism, and bacteria are by far the most abundant organisms in the plankton. Field studies show a strong correlation between viral and bacterial numbers, whereas the correlations between viruses and chlorophyll are weaker. This suggests that most viruses are bacteriophages rather than those infecting phytoplankton or other eukaryotes. However, viruses infecting cyanobacteria (*Synechococcus*) are also quite common and sometimes particularly abundant, exceeding 10^8 per liter in some cases. Even though most of the viruses probably infect prokaryotes, viruses for eukaryotic plankton are also readily found. For example, those infecting the common eukaryotic picoplankter, *Micromonas pusilla*, are sometimes quite abundant, occasionally near 10^8 per liter in coastal waters. Overall, the data suggest that most viruses from seawater infect nonphotosynthetic bacteria or archaea, but viruses infecting prokaryotic and eukaryotic phytoplankton also can make up a significant fraction of the total.

A great leap in our understanding of viral diversity has occurred with the application of molecular biological techniques. These involve the analysis of variability of DNA sequence of a single gene product (e.g., a capsid head protein, or an enzyme that makes DNA), or through a technique known as viriomics, whereby all genomes in a sample are cut up into small pieces, then all the pieces sequenced and reassembled. These studies have revealed that: (1) there is a lot of diversity of closely related viruses infecting the same or similar strains of microorganisms, a phenomenon known as 'microdiversity'; (2) RNA-containing viruses comprise a small percentage of the viral mix in oceanic waters, and are similar to viruses that infect insects and mollusks; and (3) that the diversity of viruses in a liter of seawater is astonishingly high, estimated at $>10^4$ different types for a sample from coastal California.

Virus Abundance

Total direct virus counts have been made in many planktonic environments – coastal, offshore, temperate, polar, tropical, and deep sea. Typical virus abundance is $1\text{–}5 \times 10^{10}\,\mathrm{l}^{-1}$ in rich near-shore surface waters, decreasing to about $0.1\text{–}1 \times 10^{10}\,\mathrm{l}^{-1}$ in the euphotic zone of offshore low-nutrient areas, and also decreasing with depth, by about a factor of 10. A typical deep offshore profile is shown in **Figure 3**. Seasonal changes are also common, with viruses following general changes in phytoplankton, bacteria, etc.

Virus:prokaryote ratios also provide an interesting comparison. In plankton, this ratio is typically 5–25, and commonly close to 10, even as abundance drops to low levels in the deep sea. Why this ratio stays in such a relatively narrow range is a mystery, but it does suggest a link and also tight regulatory mechanisms between prokaryotes and viruses.

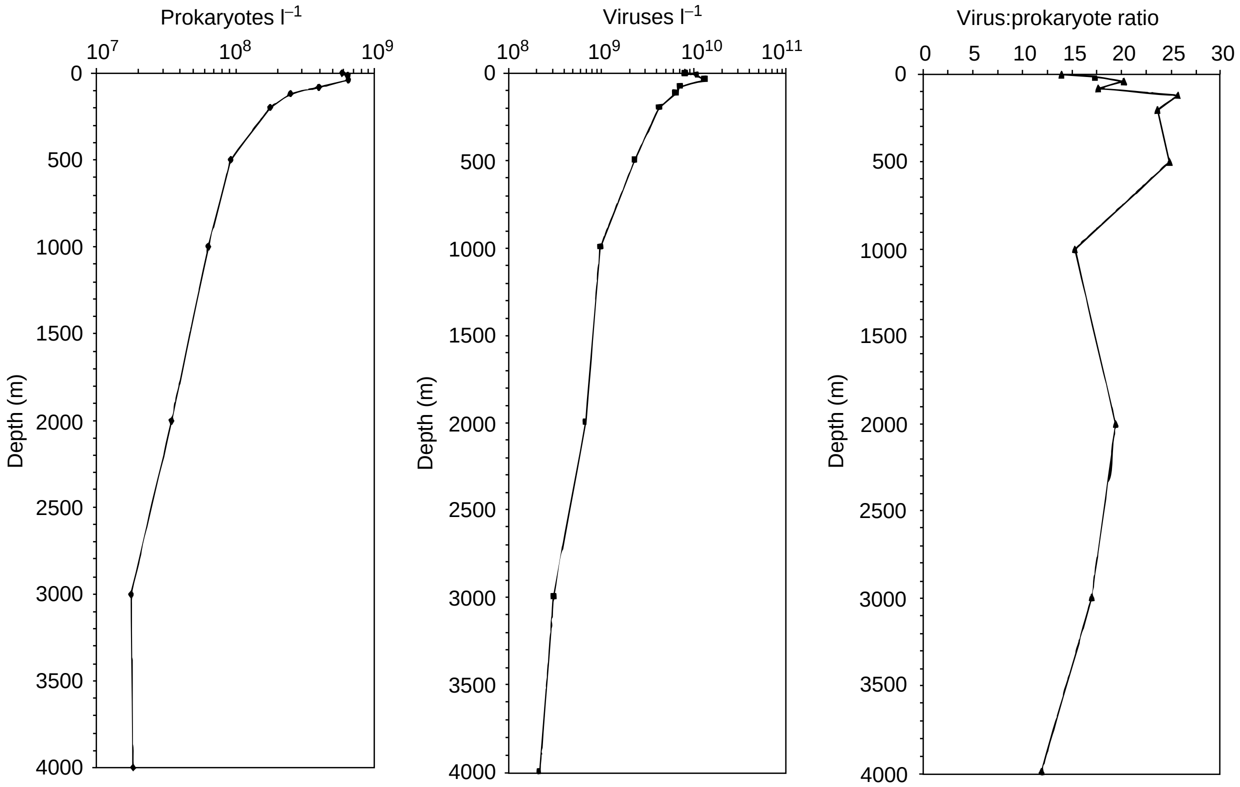

Figure 3 Depth profile of total prokaryote (bacteria–archaea) counts, total viral counts, and virus:prokaryote ratios from the Coral Sea (Apr. 1998), as determined by epifluorescence microscopy of SYBR Green-stained samples. Note the log scales of the counts.

Viral Activities

Viruses have no physical activity of their own, so 'viral activity' usually refers to lytic infection. However, before discussing such infection, lysogeny and chronic infection are considered briefly. Lysogeny, where the viral genome resides in the host's genome (**Figure 1**), is common. Lysogens (bacteria harboring integrated viral genomes) can easily be found and isolated from seawater, and lysogeny, which is linked to genetic transfer in a variety of bacteria, probably impacts microbial population dynamics and evolution. However, the induction rate appears to be low and seasonally variable under ordinary natural conditions, and lysogenic induction appears to be responsible for only a tiny fraction of total virus production in marine systems for most of the year. On the other hand, at this time we simply do not know if chronic infection is a significant process in natural systems. Release of filamentous (or other kinds of budding) viruses from native marine bacteria has not been noted in TEM studies of plankton, nor have significant numbers of free filamentous viruses (however, filamentous viruses have been observed in marine and freshwater sediments). But they could have been missed.

Regarding lytic infection, there are several studies with a variety of approaches that all generally conclude that viruses cause approximately 10–50% of total microbial mortality, depending on location, season, etc. These estimates are convincing, having been determined in several independent ways. These include: (1) TEM observation of assembled viruses within host cells, representing the last step before lysis; (2) measurement of viral decay rates; (3) measurement of viral DNA synthesis; (4) measurement of the disappearance rate of bacterial DNA in the absence of protists; (5) use of fluorescent virus tracers to measure viral production and removal rates simultaneously; and (6) direct observation of viral appearance in incubations where the viral abundance has been decreased several fold, yet host abundances remain undiluted.

Comparison to Mortality from Protists

Because the earlier thinking was that protists are the main cause of bacterial mortality in marine planktonic systems, it is useful to ask how the contribution of viruses to bacterial mortality compares to that of protists. Multiple correlation analysis of abundances of bacteria, viruses, and flagellates showed virus-induced mortality of bacteria could occasionally prevail over flagellate grazing, especially at high bacterial abundances. In more direct comparisons, measuring virus and protist rates by multiple independent approaches, the total mortality typically balances production, and viruses are found to be responsible for anything ranging from a negligible proportion to the majority of total mortality.

To sum up these studies, the consensus is that viruses are often responsible for a significant fraction of bacterial mortality in marine plankton, typically in the range 10–40%. Sometimes viruses may dominate bacterial mortality, and sometimes they may have little impact on it. It is unknown what controls this balance, but it probably includes variation in host abundance, because when hosts are less common, the viruses are more likely to be inactivated before diffusing to a suitable host, as well as the exact types of bacteria that are present and their palatability. Application of new molecular techniques, based on ribosomal RNA sequences, and variable regions within the host genomes have revealed that aquatic bacterial communities are typically dominated by a handful of bacterial taxa, while most taxa make up a tiny proportion of cell numbers. This would seem to support the notion that mostly dominant taxa are targets of viral attack.

Roles in Food Web and Geochemical Cycles

The paradigm of marine food webs has been revised a great deal in response to the initial discovery of high bacterial abundance and productivity. It is now well established that a large fraction of the total carbon and nutrient flux in marine systems passes through the heterotrophic bacteria via the dissolved organic matter. How do viruses fit into this picture? Three features of viruses are particularly relevant: (1) small size; (2) composition; and (3) mode of causing cell death, which is to release cell contents and progeny viruses to the surrounding seawater.

When a host cell lyses, the resultant viruses and cellular debris are made up of easily digested protein and nucleic acid, plus all other cellular components, in a nonsinking form that is practically defined as dissolved organic matter. This is composed of dissolved molecules (monomers, oligomers, and polymers), colloids, and cell fragments. This material is most probably utilized by bacteria as food. If it was a bacterium that was lysed in the first place, then uptake by other bacteria represents a partly closed loop, whereby bacterial biomass is consumed mostly by other bacteria. Because of respiratory losses and inorganic nutrient regeneration connected with the use of dissolved organic substances, this loop has the net effect of oxidizing organic matter and regenerating inorganic nutrients (**Figure 4**). This bacterial–viral loop effectively 'steals' production from protists that would otherwise consume the bacteria, and segregates the biomass and activity into the dissolved and smallest particulate forms. The potentially large effect has been modeled mathematically, and such models show that significant mortality from viruses greatly increases bacterial community growth and respiration rates.

Segregation of matter in viruses, bacteria, and dissolved substances leads to better retention of nutrients in the euphotic zone in virus-infected systems because more material remains in these small nonsinking forms. In contrast, reduced viral activity leads to more material in larger organisms that either sink themselves or as detritus, transporting carbon and inorganic nutrients to depth. The impact can be particularly great for potentially limiting nutrients like N, P, and Fe, which are relatively concentrated in bacteria compared to eukaryotes. At least one study has demonstrated that in cyanobacterial cultures that are starved for trace metals, the Fe in viral lysate of another culture of equal density is taken up within an hour of supplement, which suggests a major role of viral lysis in the availability of limiting nutrients. Therefore, the activity of viruses has the possible effect of helping to support higher levels of biomass and productivity in the planktonic system as a whole.

There are other potential geochemical effects of viral infection and its resultant release of cell contents to the water, owing to the chemical and physical nature of the released materials and the location in the water column where the lysis occurs. For example, polymers released from lysed cells may facilitate aggregation and sinking of material from the euphotic zone. On the other hand, viral lysis of microorganisms within sinking aggregates may lead to the breakup of the particles, converting some sinking particulate matter into nonsinking dissolved material and colloids at whatever depth the lysis occurs. This contributes to the dissolution of sinking organic matter and its availability to free-living bacteria in the ocean's interior.

Viruses, particularly lysogens, have long been known to confer to hosts the ability to produce toxins – in fact cholera toxin is only produced by the cholera bacteria when lysogenized. Through study of viriomics in marine plankton, it is now known that viral genes may encode for several geochemically important enzymes including phosphorus uptake, and components of the photosynthetic apparatus. These appear to be used both under stable host–virus

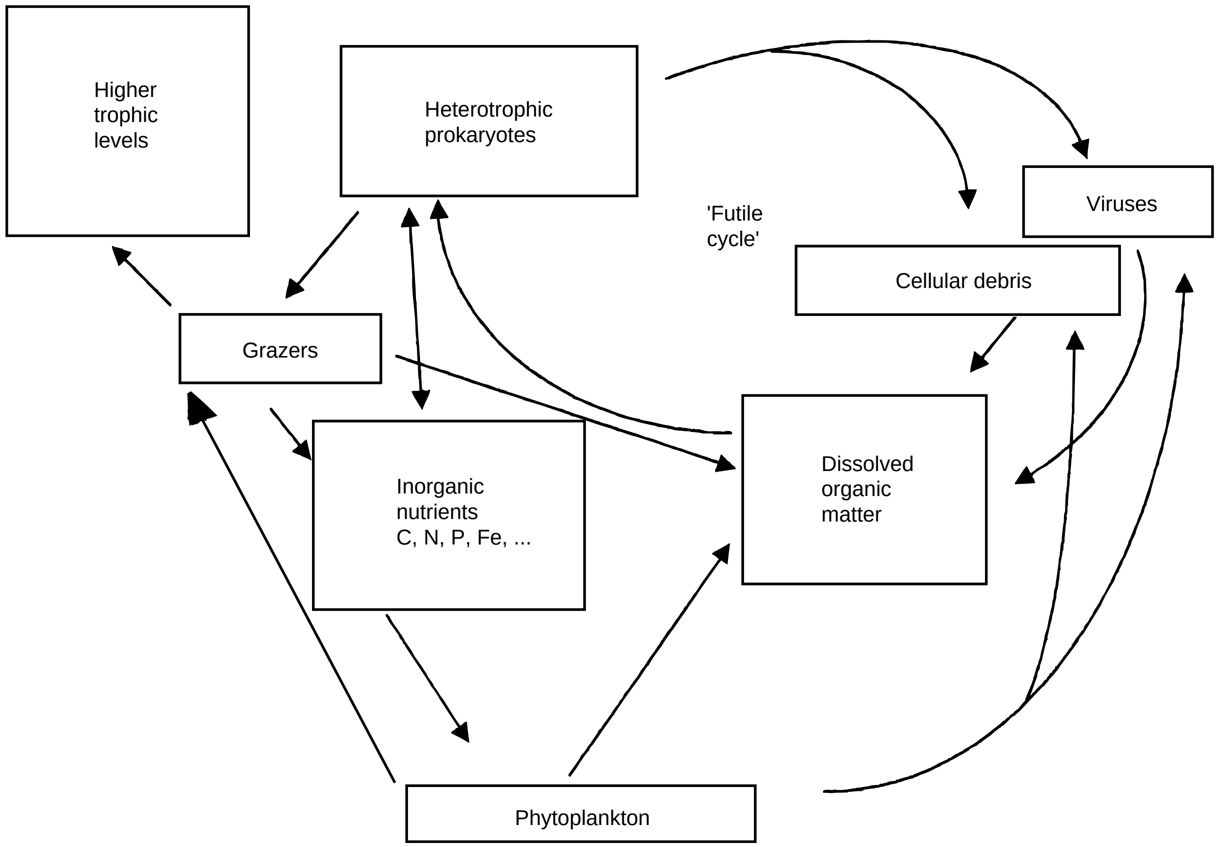

Figure 4 Prokaryote–viral loop within the microbial food web. Arrows represent transfer of matter.

conditions, as well as during host replication, when the enhanced substrate utilization capabilities inferred to hosts is used to produce new virus particles.

Effects on Host Species Compositions and Control of Blooms

Viruses mostly infect only one species or related species, and are also density dependent. Thus, the most common or dominant hosts in a mixed community are believed to be most susceptible to infection, and rare ones least so. Lytic viruses can increase only when the average time to diffuse from host to host is shorter than the average time that at least one member from each burst remains infectious. Therefore, when a species or strain becomes more abundant, it is more susceptible to infection. The end result is that viral infection works in opposition to competitive dominance. This may help to solve Hutchinson's 'paradox of plankton', which asks us how so many different kinds of phytoplankton coexist on only a few potentially limiting resources, when competition theory predicts one or a few competitive winners. Although there have been several possible explanations for this paradox, viral activity may also help solving it, because as stated above, competitive dominants become particularly susceptible to infection whereas rare species are relatively protected. Extending this argument, one might conclude that viruses have the potential to control algal blooms, such as those consisting of coccolithophorids, and so-called 'red tides' of dinoflagellates. There is now evidence that at least under some circumstances this may be true. Declining blooms have been found to contain numerous infected cells.

Along similar lines, it is now commonly thought that viral infection can influence the species composition of diverse host communities even when they are responsible for only a small portion of the host mortality. This is again because of the near-species specificity of viruses in contrast to the relatively particular tastes of protists or metazoa as grazers. This conclusion is supported by mathematical models as well as limited experimental evidence.

Resistance

The development of host resistance to viral infection is a common occurrence in laboratory and medical situations. Such resistance, where hosts mutate to resist the viral attack, is well known from nonmarine experiments with highly simplified laboratory systems. However, the existence of an apparently high infection rate in plankton suggests that the rapid development resistance is not a dominant factor in the plankton. How can the difference between laboratory and field situations be explained?

Natural systems with many species and trophic levels have far more interactions than simple laboratory systems. One might expect that a species with a large fraction of mortality from one type of virus benefits from developing resistance. However, resistance is not always an overall advantage. It often leads to a competitive disadvantage from the loss of some important receptor, for example, involved in substrate uptake. Even resistance to viral attachment, without any receptor loss, if that were possible, would not necessarily be an advantage. For a bacterium in a low-nutrient environment whose growth may be limited by N, P, or organic carbon, unsuccessful infection by a virus (e.g., stopped intracellularly by a restriction enzyme, or with a genetic incompatibility) may be a useful nutritional benefit to the host organism, because the virus injection of DNA is a nutritious boost rich in C, N, and P. Even the viral protein coat, remaining outside the host cell, is probably digestible by bacterial proteases. From this point of view, one might even imagine bacteria using ‘decoy’ virus receptors to lure viral strains that cannot successfully infect them. With the proper virus and host distributions, the odds could be in favor of the bacteria, and if an infectious virus (i.e., with a protected restriction site) occasionally gets through, the cell line as a whole may still benefit from this strategy.

There are other reasons why resistance might not be an overall advantage. As described earlier, model results show that the heterotrophic bacteria as a group benefit substantially from viral infection, raising their production by taking carbon and energy away from larger organisms. Viruses also raise the overall system biomass and production by helping to keep nutrients in the lighted surface waters. However, these arguments would require invoking some sort of group selection theory to explain how individuals would benefit from not developing resistance (i.e., why not ‘cheat’ by developing resistance and letting all the other organisms give the group benefits of infection?). In any case, evidence suggests that even if resistance of native communities to viral infection may be common, it is not a dominant force, because there is continued ubiquitous existence of viruses at roughly 10 times greater abundance than bacteria and with turnover times on the order of a day (as discussed above). Basic mass balance calculations show that significant numbers of hosts must be infected and releasing viruses all the time. For example, with a typical lytic burst size of 50 and viral turnover time of 1 day, maintenance of a 10-fold excess of viruses over bacteria requires 20% of the bacteria to lyse daily. The lack of comprehensive resistance might be due to frequent development of new virulent strains, rapid dynamics or patchiness in species compositions, or to a stable coexistence of viruses and their hosts. All these are possible, and they are not mutually exclusive.

Lysogeny, which is common in marine bacterioplankton, also conveys resistance to superinfection (i.e., infection by the same, or similar virus). This may be an advantage so long as the prophage remains uninduced, in that viral genomes often also contain useful genes involved in membrane transport, photosynthesis, etc., that benefit the host. However, because the prophage is carried around in the host cell, this may also place an extra burden on the host cell machinery (i.e., it must also replicate the viral genome in addition to the host genome).

Genetic Transfer

Viruses can also play central roles in genetic transfer between microorganisms, through two processes. In an indirect mechanism, viruses mediate genetic transfer by causing the release of DNA from lysed host cells that may be taken up and used as genetic material by another microorganism. This latter process is called transformation. A more direct process is known as transduction, where viruses package some of the host’s own DNA into the phage head and then inject it into another potential host. Transduction in aquatic environments has been shown to occur in a few experiments. Although transduction usually occurs within a restricted host range, recent data indicate that some marine bacteria and phages are capable of transfer across a wide host range. Although the extent of these mechanisms in natural systems is currently unknown, they could have important roles in population genetics, by homogenizing genes within a potential host population, and also on evolution at relatively long timescales. Gene transfer across species lines is an integral component of microbial evolution, as shown in the genomes of modern-day microbes that contain numerous genes that have obviously been transferred from other species. On shorter timescales, this process can be responsible for the dissemination of genes that may code for novel properties, whether introduced to native communities naturally or via genetic engineering.

Summary

It is now known that viruses can exert significant control of marine microbial systems. A major effect is on mortality of bacteria and phytoplankton, where viruses are thought to stimulate bacterial activity at the expense of larger organisms. This also stimulates the entire system via improved retention of nutrients in the euphotic zone. Other important roles include influence on species compositions and possibly also genetic transfer.

See also

Bacterioplankton. Primary Production Distribution. Primary Production Methods. Primary Production Processes.

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BACTERIOPLANKTON

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Introduction

Marine bacteria, unicellular prokaryotic plankton usually less than 0.5–1 μm in their longest dimension, are the smallest autonomous organisms in the sea – or perhaps in the biosphere. The nature of their roles in marine food webs and the difficulty of studying them both stem from their small size. A modern paradigm for bacterioplankton ecology was integrated into oceanography only following development of modern epifluorescence microscopy and the application of new radioisotopic tracer techniques in the late 1970s. It was not until a decade later, with the use of modern genomic techniques, that their identity and taxonomy began to be understood at all. Thus we are still in the process of constructing a realistic picture of marine bacterial ecology, consistent with knowledge of evolution, plankton dynamics, food web theory, and biogeochemistry. The lack of bacterioplankton compartments in most numerical models of plankton ecology testifies to out current level of ignorance. Nevertheless, much is now well known that was just beginning to be guessed in the 1980s.

Bacterioplankton are important in marine food webs and biogeochemical cycles because they are the principal agents of dissolved organic matter (DOM) utilization and oxidation in the sea. All organisms liberate DOM through a variety of physiological processes, and additional DOM is released when zooplankton fecal pellets and other forms of organic detritus dissolve and decay. By recovering the released DOM, which would otherwise accumulate, bacterioplankton initiate the microbial loop, a complicated suite of organisms and processes based on the flow of detrital-based energy through the food web. The flows of energy and materials through the microbial loop can rival or surpass those flows passing through traditional phytoplankton-grazer-based food chains. For further information on the topics summarized here, the reader may consult the Further Reading, especially the recent book edited by Kirchman.

Identity and Taxonomy

Most bacterial species cannot be cultivated in the laboratory and, until the development of culture-independent genomic methods, the identity of over 90% of bacterial cells enumerated under the microscope was unknown. Only those few cells capable of forming colonies on solid media (agar plates) could be identified by classical bacteriological techniques. However, since the application of molecular genomic methods to sea water samples in the mid-1980s, our understanding of marine bacterial systematics and evolution has undergone a profound revolution. In this approach, plankton samples including bacterioplankton cells are collected and lysed to yield a mixture of DNA strands reflecting the genetic composition of the original assemblage. Then individual genes on the DNA molecules can be cloned and amplified via the polymerase chain reaction (PCR) for further analysis. Theoretically, any gene complex can be cloned, and several major groups of genes have been studied to date – for example, genes controlling specific biogeochemical transformations like ammonium oxidation, nitrogen fixation, sulfate reduction, and even oxidation of xenobiotic pollutant molecules. The most useful and widely studied genes for elucidating evolutionary relationships among bacterioplankton have been the genes coding for small subunit ribosomal RNA (SSU rRNA), because they evolve relatively slowly and their characters have been conserved across all life forms during the course of evolution. By sequencing the base pairs making up individual SSU rRNA molecules, the similarity of different genes can be established with great sensitivity. To date, nearly 1000 individual microbial SSU rRNA genes have been cloned and sequenced, yielding an entirely new picture of the composition of marine communities.

The most important aspect of our understanding is that what we term ‘bacterioplankton’ really consists of two of the fundamental domains of life: the *Bacteria* and the *Archaea* (Figure 1). Domain *Archaea* is a group of microbial organisms with unique genetic, ultrastructural, and physiological characters that are about as different, genetically, from the *Bacteria* as either group is from higher life forms. Members of the *Archaea* may be typified by organisms from extreme habitats including anaerobic environments, hot springs, and salt lakes, but marine archaeal groups I and II are common in sea water. They make up about 10% of the microbial plankton in the

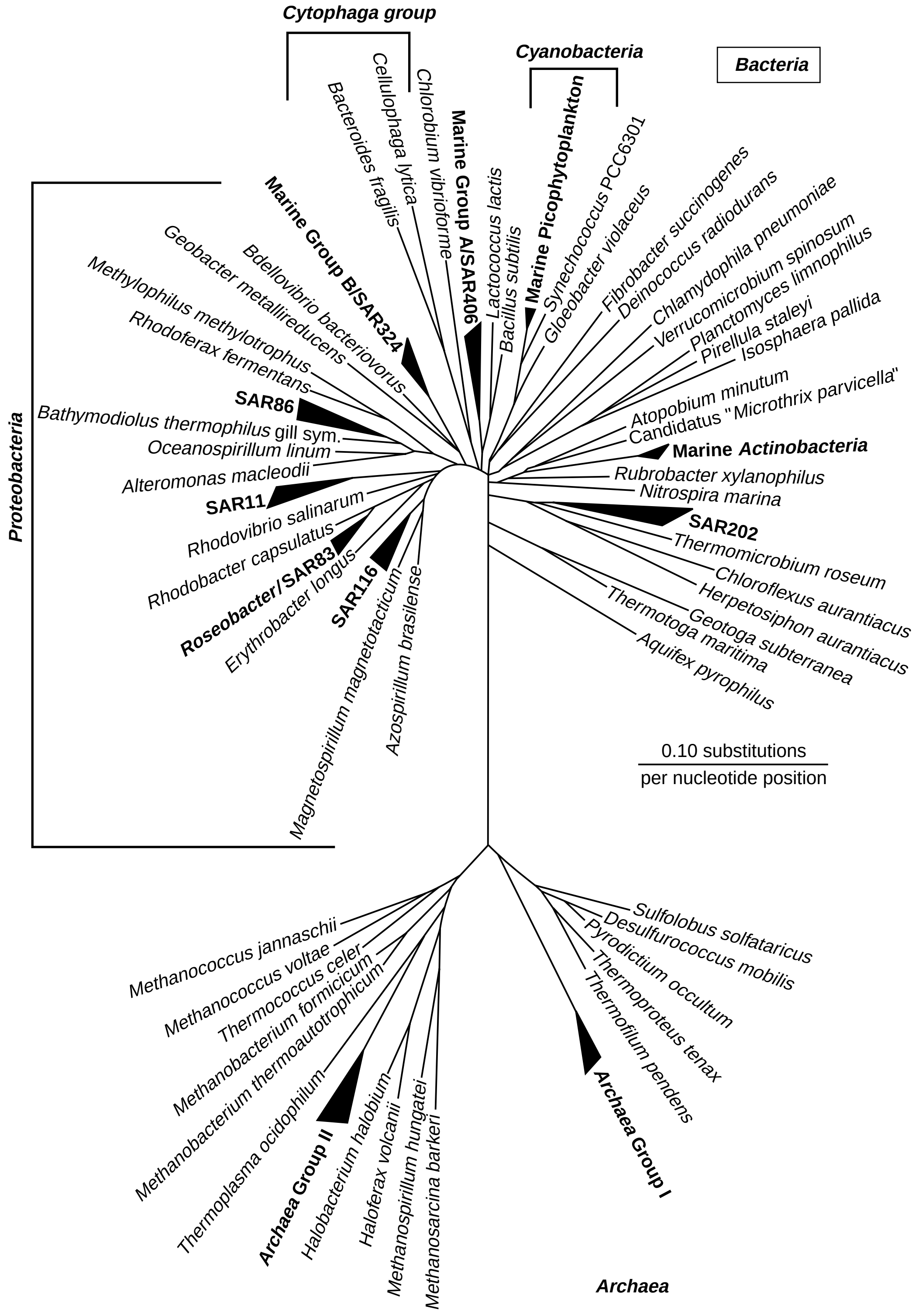

Figure 1 Dendrogram showing relationships among the most widespread SSU rRNA gene clusters among the marine prokaryotes (the 'bacterioplankton'). (Modified after Giovannoni SJ, in Kirchman (2000).)

surface waters of the oceans, and are relatively more numerous at greater depths, where they approach about half the total abundance. Since most of these organisms are known only from their RNA genes and have never been cultured, their physiology and roles in the plankton are almost entirely unknown.

Domain *Bacteria* contains all the familiar, culturable eubacterial groups and also a large number of unculturable, previously unknown groups. The main culturable groups include members of the *Proteobacteria*, marine oxygenic, phototrophic *Cyanobacteria*, and several other major groups including methylotrophs, planctomycetes, and the *Cytophaga–Flavobacterium–Bacteroides* group. But the most abundant genes recovered so far are not similar to those of the known culturable species. These include the most ubiquitous of all groups yet recovered, the SAR-11 cluster of the alpha *Proteobacteria*, which have been recovered from every bacterial clone library yet isolated. It appears to be the most widely distributed and successful of the *Bacteria*. The photosynthetic *Cyanobacteria*, including *Synecchococcus* spp. and the unicellular prochlorophytes, are functionally phytoplankton and they dominate the primary producer populations in the open sea, and at times in coastal and even estuarine regimes. They are treated elsewhere in this encyclopedia, so our discussion here is limited to heterotrophic forms of *Bacteria* and to the planktonic *Archaea*, although we cannot specify what many (or most) of them do. Genomic techniques are now being used to investigate bacterial and archaeal species succession during oceanographic events over various timescales, much as phytoplankton and higher organism successions have been observed for a century or more.

Nutrition and Physiology

Knowledge of the nutrition and physiology of naturally occurring bacterioplankton as a functional group in the sea is based partly on laboratory study of individual species in pure culture, but mostly on sea water culture experiments. Traditional laboratory investigations show that bacteria can only utilize small-molecular-weight compounds less than ~500 Daltons. Larger polymeric substances and particles must first be hydrolyzed by extracellular enzymes. In the sea water culture approach, samples with natural bacterioplankton assemblages are incubated for suitable periods (usually hours to a few days) while bacterial abundance is monitored, the utilization of various compounds with ^{14}C- or ^{3}H-labelled radiotracers is estimated, and the net production or loss of metabolites like oxygen, CO_2, and inorganic nutrients is measured. Such experiments, combined with size-fractionation using polycarbonate filters with precise and uniform pores of various diameter (0.2–10 μm), revealed that over 90% of added organic radiotracers are utilized by the smallest size fractions (<1 μm). Bacteria are overwhelmingly the sink for DOM in all habitats studied to date. Nutrient limitation of bacterial growth can be identified by adding various compounds (e.g., ammonium, phosphate, or iron salts; monosaccharides and amino acids) singly or in combination to experimental treatments and comparing growth responses to controls. Using this approach, it has been learned that bacteria are effective competitors with phytoplankton for inorganic nutrients, including iron, which bacteria can mobilize by producing iron-binding organic complexes called siderophores. In general, bacterial growth in the sea, from estuaries to the central gyres, tends to be limited by organic matter. Sea water cultures most often respond to additions of sugars and amino acids, with the response sometimes enhanced if inorganic nutrients (including iron) are also added.

At larger scales, the ultimate dependence of bacteria on organic matter supply is indicated by significant correlations between bacterial standing stocks or production (see below) and primary production (PP) across habitats (Figure 2). At within-habitat scales and shorter timescales, significant relationships are less common, indicating time lags between organic matter production and its conversion by bacteria. Such uncoupling of organic matter production and consumption is also shown by transient accumulations of DOM in the upper ocean, where production processes tend to exceed utilization. It is not yet understood why DOM accumulates. Some fraction might be inherently refractory or rendered so by ultraviolet radiation or chemical condensation reactions in sea water. Deep ocean

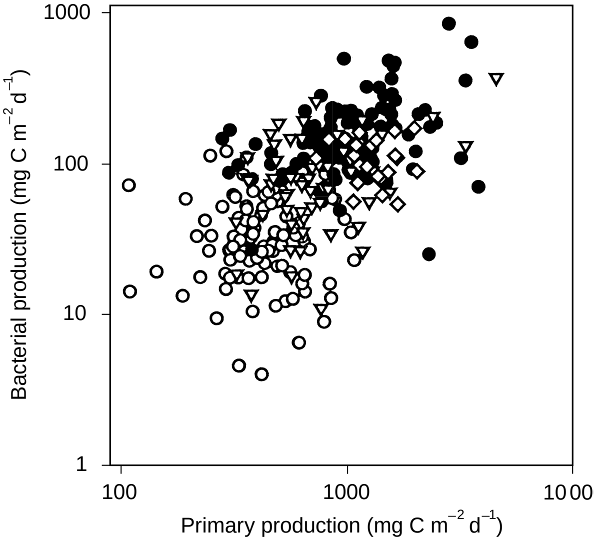

Figure 2 Bacterial production plotted against primary production for the euphotic zone in several major ocean regimes or provinces. The overall data set has a significant regression, but the individual regions do not. ○, Sargasso Sea; ●, Arabian Sea; ◇, equatorial Pacific; △, equatorial Pacific.

DOM has a turnover time of centuries to millennia, and seems to become labile (vulnerable to bacterial attack) when the ocean thermohaline circulation returns it to the illuminated surface layer. Alternatively, bacterial utilization of marine DOM, which generally has a high C:N ratio, might be limited by availability of inorganic nutrients. The latter hypothesis is supported by observations that DOM accumulation tends to be greater in the tropics and subtropics, where nitrate and phosphate are depleted in surface waters.

The efficiency with which bacteria convert organic matter (usually expressed in carbon units) into biomass can be estimated by comparing the apparent utilization of individual compounds or bulk DOM with increases in biomass or with respiration. Respiration is usually measured by oxygen utilization but precise new analytical techniques for measuring carbon dioxide make CO_2 production a preferable approach. Bacterial respiration (BR) is difficult to measure because water samples must first be passed through filters to remove other, larger respiring organisms, and because the resulting respiration rates are low, near the limits of detection of oxygen and CO_2 analyses. It is also not easy to estimate bacterial biomass precisely (see below). The conversion efficiency or bacterial growth efficiency (BGE) is the quotient of net bacterial production (BP) and the DOM utilization:

$$\mathrm{BGE} = \frac{\mathrm{BP}}{\Delta\mathrm{DOM}} = \frac{\mathrm{BP}}{\mathrm{BP} + \mathrm{BR}} \qquad [1]$$

Bacteria have rather uniform biomass C:N composition ratios of 4–6. Intuitively, it seems reasonable to expect that they would utilize substrates with high C:N ratios at lower efficiency. Enrichment cultures initiated from natural bacterial assemblages grow in sea water culture in the laboratory on added substances with efficiencies of 30–90%. The BGE is inversely related to the C:N ratio of the organic substrate if just a single compound is being utilized, but when a mixture of compounds is present, as is probably always the case in the environment, there is no discernible relationship between the chemical composition of the materials being used and the BGE.

In the open ocean, BGE averages about 10–30%, a relatively low value that has important implications for our understanding and modeling of organic matter turnover and ocean metabolism. At larger scales, BGE appears to increase from $\sim 10\%$ to 50% along an offshore-to-onshore gradient of increasing primary productivity, probably reflecting greater organic matter availability. This pattern has been used to support an argument suggesting that in lake and oceanic systems with the lowest primary productivity, respiration exceeds production; that is, such oligotrophic systems might be net heterotrophic. This possibility has also been supported by results from careful light–dark bottle studies in which oxygen consumption exceeds production. This finding, however, is inconsistent with a large amount of geochemical evidence, for instance showing net oxygen production at the basin and seasonal to annual scale. Resolution of this debate probably rests on improved estimates of BGE.

Pure culture, sea water culture, and the latest genomic studies indicate fundamental metabolic and genetic differences among different bacterial populations, which can generally be grouped into two broad classes based on organic matter utilization. Native marine bacteria capable of utilizing DOM at concentrations below $100\,\mathrm{nmol\ l^{-1}}$, termed oligotrophs, cannot survive when DOM is greater than about 0.1–$1\,\mathrm{mmol\ l^{-1}}$. Copiotrophic bacteria found in some habitats with higher ambient DOM levels thrive on concentrations far exceeding this threshold. Observations that copiotrophs shrink and have impressive survival capability under severe starvation conditions (thousands of days to, apparently, centuries) led some investigators to suggest that the dominant native marine bacteria are starving (nongrowing) copiotrophs in a survival mode, awaiting episodes of nutrient enrichment. A variable fraction of the total population usually does appear to be dormant, as indicated by autoradiography, vital staining, and RNA probes, but the timescales of the transition from active growth to dormancy and back again are not well defined. Maintenance of dormant cells in a population depends on strong predator preferences for actively growing cells and prey selection against the nongrowing cells. Most oligotrophs so far isolated in the laboratory under stringent low-DOM conditions appear to be unrelated to known bacterial groups.

Bacterial Biomass, Growth, and Production

The standing stock of bacteria is still most commonly assessed by epifluorescence microscopy, following staining of the cells with a fluorochrome dye. Flow cytometric determination is gradually taking over, and has several key advantages over microscopy: faster sample processing, improved precision, and discrimination of heterotrophic and phototrophic bacteria. There is a gradient in bacterial abundance proceeding from $\sim 10^{10}$ cells $\mathrm{l^{-1}}$ in estuaries to 10^{9}

cells l^{-1} in productive ocean regimes and 10^8 cells l^{-1} in the oligotrophic gyres (Figure 3). These horizontal gradients parallel gradients in primary production and organic matter fluxes, suggesting the overall importance of bottom-up controls on bacterial abundance. Chlorophyll *a* concentrations, indicative of phytoplankton biomass, vary somewhat more widely than bacterial abundance over basin to global scales, but within habitats, the variability of bacterial and phytoplankton biomass is about equal, reflecting the generally close coupling between the two groups and the similarity of removal processes (grazing, viral lysis, unspecified mortality) acting on them.

It is more difficult to estimate bacterial biomass, because we cannot measure the mass (e.g., as carbon) directly, and have to convert estimates of cell volumes to carbon instead. The best estimates now indicate $7\text{–}15 \times 10^{-15}$ g C cell^{-1} for oceanic cells and $15\text{–}25 \times 10^{-15}$ g C cell^{-1} for the slightly larger cells found in coastal and estuarine habitats. Thus the biomass gradient is steeper than the abundance gradient because the cells are larger inshore. Table 1 shows data compiled from Chesapeake Bay and the Sargasso Sea off Bermuda, two well-studied sites that illustrate the contrasts in phytoplankton and bacterioplankton from a nutrient-rich estuary to the oligotrophic ocean gyres. Bacterial and phytoplankton biomass are much greater in the estuary, as expected. Interestingly, assuming a mean euphotic zone depth of 1 m in the Bay and 140 m off Bermuda, we find that the standing stocks of bacteria in these euphotic zones are ~10 and 50 mmol C m^{-2} in the estuaries and open sea, respectively. The oceanic euphotic zone is somewhat more enriched in bacteria than the more productive estuaries. Bacterial and phytoplankton stocks are nearly equal in the open sea, but phytoplankton exceeds bacterial biomass inshore. Carbon from primary producers appears to be more efficiently stored in bacteria in oceanic systems compared to estuarine ones.

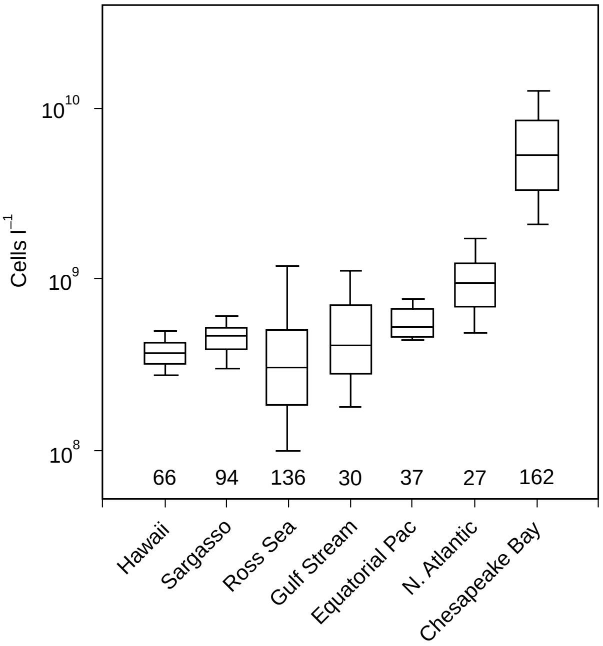

Figure 3 Bacterial abundance in the euphotic zone of several major ocean provinces. The box plots show the median, 10th, 25th, 75th and 90th centiles of the data. The number of samples is listed for each region. There is no statistical difference among the regions except for Chesapeake Bay.

Bacterial stocks in different environments can be assessed using the relationship

$$B_{\max} = F/m \qquad [2]$$

where $B_{\max}$ is the carrying capacity in the absence of removal, F is the flux of utilizable organic matter to the bacteria, and m is their maintenance efficiency (the specific rate of utilization when all of F is used to meet cellular maintenance costs, with nothing left for growth). The problem is specifying values for F and m. The DOM flux can be evaluated by flow analysis and is about 20–50% of the net primary production (NPP) in most systems. Maintenance costs are poorly constrained and possibly very low if most cells are near a starvation state, but 0.01 d^{-1} is a reasonable value for actively growing cells. Thus for the oligotrophic gyres where the latest NPP estimates are about 200–400 mg C m^{-2} d^{-1}, we can calculate that $B_{\max}$ should be about $4\text{–}8 \times 10^9$ cells l^{-1}, an order of magnitude greater than observed. Removal processes must maintain bacterial stocks considerably below their maximum carrying capacity.

Bacteria convert preformed organic matter into biomass. This process is bacterial production, which can be expressed as the product of the biomass and the specific growth rate (μ)

$$\mathrm{BP} = \mathrm{d}B/\mathrm{d}t = \mu B \qquad [3]$$

Like biomass, BP cannot be measured directly in mass units. Instead, metabolic processes closely coupled to growth are measured and BP is derived using conversion factors. The two most common methods follow DNA and protein synthesis using (^{3}H)thymidine and (^{3}H)leucine incorporation rates, respectively. The values for the conversion factors are poorly constrained and hard to measure, leading to uncertainty of at least a factor of two in the BP estimates. Few measurements were performed in the open sea before the 1990s. The Joint Global Ocean Flux Study (JGOFS) time-series station at Bermuda is perhaps the best-studied site in the ocean (Table 1).

Table 1 The biomass (*B*) and production rates (*P*) of bacterioplankton and phytoplankton at estuarine and open ocean locations[a]

	Biomass (mmol m^{-3})		*Production rate (mmol m^{-3} d^{-1})*		*P/B (d^{-1})*	
Location	*Phytoplankton*	*Bacteria*	*Phytoplankton*	*Bacteria*	*Phytoplankton*	*Bacteria*
Chesapeake Bay	5–400 (56)	1–80 (11)	20–47 (33)	0.1–50 (4)	0.07–1.9	0.01–2 (0.34)
Sargasso Sea	0.3–3.2 (1.0)	0.2–0.6 (0.4)	0.06–0.9 (0.3)	0.002–0.07 (0.02)	0.1–1 (0.3)	0.01–0.16 (0.06)

[a] The values are annual, euphotic zone averages derived from published reports. P/B is the specific turnover rate for the population. The data are presented as ranges with the mean of various estimates in parentheses. Ranges encompass observations and assumptions about conversion factors for deriving values from measurements (see text).

In the open sea, far removed from allochthonous inputs of organic matter, we can compare BP and PP directly, since all the organic matter ultimately derives from the PP. One difficulty is that BP itself is not constrained by PP, since if the recycling efficiency of DOM and the BGE are sufficiently high, BP can exceed PP. BP also commonly exceeds local PP in estuaries, where inputs of terrestrial organic matter are consumed by bacteria. Bacterial respiration, however, cannot exceed the organic matter supply and serves as an absolute constraint on estimates of BP. But as noted above, bacterial respiration is very hard to measure and there are many fewer reliable measurements than for BP itself. BR is usually estimated from the BGE. Rearranging eqn [1],

$$\mathrm{BR} = \frac{(1 - \mathrm{BGE})\mathrm{BP}}{\mathrm{BGE}} \qquad [4]$$

Most commonly, variations of eqn [1] have been used to estimate the total bacterial carbon utilization or demand (BCDBR + BP) from estimates or assumptions about BP and BGE. Earlier estimates and literature surveys suggested that BP was as high as 30% of PP. Combining this value with a BGE of 20% yields a BCD of 1.5 times the PP. This estimate in itself is possibly acceptable, if recycling of DOM is high, but then eqn [4] yields a BR of 1.2 times the total PP – an impossibility. More recent estimates of BP, typified by the Sargasso Sea data, suggest BP is about 10% of PP in the open sea. Applying this value and the mean BGE for the region (0.14), we find that BR consumes about 55% of the primary production in the Sargasso Sea, still a substantial figure. Similar calculations for other well-studied ocean areas suggest that zooplankton (including protozoans and microzooplankton) and bacteria consume nearly equal amounts of the total primary productivity. These estimates illustrate the biogeochemical importance of bacterioplankton in the ocean carbon cycle: although their growth efficiency is low, bacteria process large amounts of DOM. DOM produced by a myriad of ecological and physiological processes must escape bacterial metabolism to enter long-term storage in the oceanic reservoir.

Role in Food Webs and Biogeochemical Cycles

The process of bacterivory (consumption of bacteria by bacteriovores) completes the microbial loop. Bacterioplankton cells are ingested by a great diversity of predators, but, because of the small size of the prey, most bacteriovores are small protozoans, typically $<5\,\mu$m nanoflagellates and small ciliates. Bacterial cells only occupy about 10^{-7} of the volume of the upper ocean, indicating the difficulty of encountering these small prey. Larger flagellates, small ciliates, and some specialized larger predators can also ingest bacterial prey. The most important of the larger predators are gelatinous zooplankton like larvaceans, which use mucus nets to capture bacterial cells sieved from suspension. But most bacteriovores are also very small. Nanoflagellates can clear up to 10^5 body volumes per hour, thus making a living from harvesting small, rare bacterial prey, and generally dominating bacterivory in the sea. Protozoan bacterivory closely balances BP in less-productive oceanic regimes. Most crustacean zooplankton cannot efficiently harvest bacterioplankton unless the latter are attached to particles, effectively increasing their size. Bacterial prey enter marine food webs following ingestion by flagellates, and ingestion of the flagellates by other flagellates, ciliates, and copepods. This means that bacteria usually enter the higher trophic levels after several cycles of ingestion by consumers of increasing size, with attendant metabolic losses at each stage. The microbial loop and its characteristic long, inefficient food chains can be short-circuited by the gelatinous bacteriovores, which package bacterial cells into larger prey.

Compared to phytoplankton and to bacteriovores, bacteria are enriched relative to body carbon in nitrogen, phosphorus, protein, nucleic acids, and iron. Their excess nutritional content, coupled with the many trophic exchanges that bacterial biomass passes through as it moves in food webs, means that the microbial loop is primarily a vehicle for nutrient regeneration in the sea rather than an important source of nutrition for the upper trophic levels. The main function of bacteria in the microbial loop is to recover 'lost' DOM, enrich it with macro- and micronutrients, and make it available for regeneration and resupply to primary producers. Lower bacterial production estimates (see above) would also tend to decrease the importance of bacteria as a subsidy for higher consumers.

In estuaries and other shallow near-shore habitats, BP is not as closely balanced by planktonic bacteriovores as in ocean systems. In these productive habitats, bacteria are larger and more often associated with particles, so they are vulnerable to a wider range of grazers. Bacteria can also be consumed by mussels, clams, and other benthic suspension feeders. External subsidies of organic matter mean that BP is higher inshore, so bacteria are a more important food source in coastal and estuarine food webs than in oceanic waters. In these productive systems where bacterial abundance is greater, more of the bacterial stock is also attacked and lysed by viruses, resulting in release of DOM and nutrients instead of entry into food webs. The relative importance of viruses and bacteriovores in removing bacteria is not yet well known, but has important implications for food web structure.

Bacteria are the major engines of biogeochemical cycling on the planet, and serve to catalyze major transformations of nitrogen and sulfur as well as of carbon. They participate in the carbon cycle in several ways. Their principal role is to serve as a sink for DOM, and thus regulate the export of DOM from the productive layer. Bacteria also have intensive hydrolytic capability and participate in decomposition and mineralization of particles and aggregates. Bacteria rapidly colonize fresh particulate matter in the sea, and elaborate polymeric material that helps to cement particles together, so they both reduce particle mass by enzymatic hydrolysis and promote particle formation by fostering aggregation. The balance of bacterial activity for forming particles and accelerating particle sedimentation or, in contrast, decomposing particles and reducing it, is not clear. Larvaceans and other giant, specialized bacteriovores, centimeters to meters in size, can repackage tiny bacterial cells into large, rapidly sinking fecal aggregates, thus feeding the ocean's smallest organisms into the biological carbon pump.

Conclusions

Knowledge of the dynamics of bacterioplankton, their identity, roles in food webs and biogeochemical cycles is now becoming better known and integrated in a general theory of plankton dynamics, but these aspects are not yet common in plankton ecosystem models. The differential importance of bacteria in plankton food webs in coastal and oceanic systems might serve as a good test of our understanding in models. The dynamics of DOM are only crudely parametrized in most models, and explicit formulation of bacterial DOM utilization may help in better characterizing DOM accumulation and export. Other interesting problems such as the effects of size-selective predation, bacterial community structure, and species succession are just beginning to be explored. Exploration of marine bacterial communities together with molecular probes and numerical models should lead to a new revolution in plankton ecology.

See also

Copepods. Marine Mammal Trophic Levels and Interactions. Primary Production Methods. Primary Production Processes. Protozoa, Planktonic Foraminifera. Protozoa, Radiolarians.

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PROTOZOA, RADIOLARIANS

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Introduction

Radiolarians are exclusively open ocean, silica-secreting, zooplankton. They occur abundantly in major oceanic sites worldwide. However, some species are limited to certain regions and serve as indicators of water mass properties such as temperature, salinity, and total biological productivity. Abundances of total radiolarian species vary across geographic regions. For example, maximum densities reach 10 000 per m^3 in some regions such as the subtropical Pacific. By contrast, densities range about 3–5 per m^3 in the Sargasso Sea. Radiolarians are classified among the Protista, a large and eclectic group of eukaryotic microbiota including the algae and protozoa. Algae are photosynthetic, single-celled protists, while the protozoa obtain food by feeding on other organisms or absorbing dissolved organic matter from their environment. Radiolarians are single-celled or colonial protozoa. The single-celled species vary in size from $<100\,\mu m$ to very large species with diameters of 1–2 mm. The larger species are taxonomically less numerous and include mainly gelatinous species found commonly in surface waters. The smaller species typically secrete siliceous skeletons of remarkably complex design (Figure 1). The skeletal morphology is species-specific and used in taxonomic identification. Larger, noncolonial species are either skeletonless, being enclosed only by a gelatinous coat, or produce scattered siliceous spicules within the peripheral cytoplasm and surrounding gelatinous layer. Colonial species contain numerous radiolarian cells interconnected by a network of cytoplasmic strands and enclosed within a clear, gelatinous envelope secreted by the radiolarian. The colonies vary in size from several centimeters to nearly a meter in length. The shape of the colonies is highly variable among species. Some are spherical, others ellipsoidal, and some are elongate ribbon-shaped or cylindrical forms. These larger species of radiolarians are arguably, the most diverse and largest of all known protozoa. Many of the surface-dwelling species contain algal symbionts in the peripheral cytoplasm that surrounds the central cell body. The algal symbionts provide some nutrition to the radiolarian host by secretion of photosynthetically produced organic products. The food resources

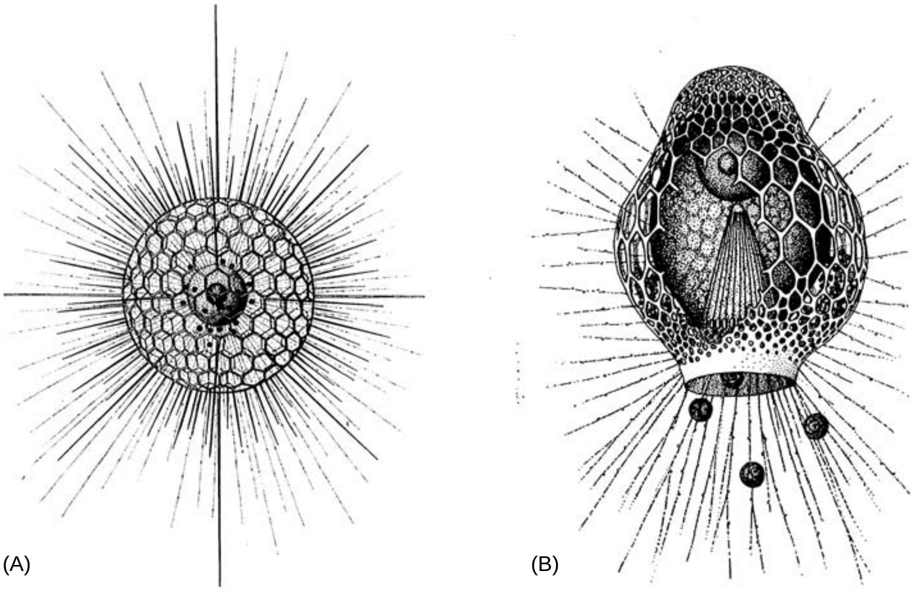

Figure 1 Morphology of polycystine radiolaria. (A) Spumellarian with spherical central capsule and halo of radiating axopodia emerging from the fusules in the capsular wall and surrounded by concentric, latticed, siliceous shells. (B) Nassellarian showing the ovate central capsule with conical array of microtubules that extend into the basally located fusules and external axopodia protruding from the opening of the helmet-shaped shell. Reproduced with permission from Grell K (1973) *Protozoology*. Berlin: Springer-Verlag.

are absorbed by the radiolarian and, combined with food gathered from the environment, are used to support metabolism and growth. Radiolarians that dwell at great depths in the water column where light is limited or absent typically lack algal symbionts. The siliceous skeletons of radiolarians settle into the ocean sediments where they form a stable and substantial fossil record. These microfossils are an important source of data in biostratigraphic and paleoclimatic studies. Variations in the number and kind of radiolarian species (based on skeletal form) in relation to depth in the sediment provide information about climatic and environmental conditions in the overlying water mass at the time the radiolarian skeletons were deposited at that geographic location. The radiolarians are second only to diatoms as a major source of biogenic opal (silicate) deposited in the ocean sediments.

Cellular Morphology

The radiolarian cell body contains a dense mass of central cytoplasm known as the central capsule (Figure 2). Among the organelles included in the central capsule are the nucleus, or nuclei in species with more than one nucleus, most of the food reserves, major respiratory organelles, i.e., mitochondria, Golgi bodies for intracellular secretion, protein-synthesizing organelles, and vacuoles. The central capsule is surrounded by a nonliving capsular wall secreted by the radiolarian cytoplasm. The thickness of the capsular wall varies among species. It may be thin or in some species very reduced, consisting of only a sparse deposit of organic matter contained within the surrounding cytoplasmic envelope. In others, the wall is quite thick and opalescent with a pearl-like appearance. The capsular wall contains numerous pores through which cytoplasmic strands (fusules) connect to the extracapsular cytoplasm. The extracapsular cytoplasm usually forms a network of cytoplasmic strands attached to stiffened strands of cytoplasm known as axopodia that extend outward from the fusules in the capsular wall. The central capsular wall and axopodia are major defining taxonomic attributes of radiolarians. A frothy or gelatinous coat typically surrounds the central capsule and supports the extracapsular cytoplasm. Algal symbionts, when present, are enclosed within perialgal vacuoles produced by the extracapsulum. In most species, the algal symbionts are exclusively located in the extracapsulum. Thus far, symbionts have been observed within the central capsular cytoplasm in only a few species. Food particles, including small algae and protozoa or larger invertebrates such as copepods, larvacea, and crustacean larvae, are captured by the sticky rhizopodia of the extracapsulum. The cytoplasm moves by cytoplasmic streaming to coat and enclose the captured prey. Eventually, the prey is engulfed by the extracapsular cytoplasm and digested in digestive vacuoles (lysosomes). These typically accumulate in the extracapsulum near the capsular wall. Large prey such as copepods are invaded by flowing strands of cytoplasm and the more nutritious soft parts such as muscle and organ tissues are broken apart, engulfed within the flowing cytoplasm and carried back into the extracapsulum where digestion takes place. The siliceous skeleton, when present, is deposited within cytoplasmic spaces formed by extensions of the rhizopodia. This elaborate framework of skeletal-depositing cytoplasm is known as the cytokalymma. Thus, the form of the skeleton is dictated by the dynamic streaming and molding action of the cytokalymma during the silica deposition process. Consequently, the very elaborate and species-specific form of the skeleton is determined by the dynamic activity of the radiolarian and

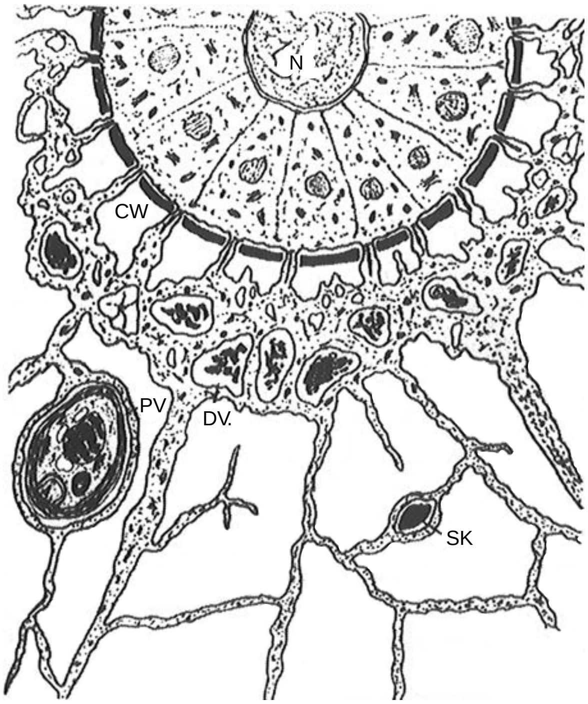

Figure 2 Cytoplasmic organization of a spumellarian radiolarian showing the central capsule with nucleus (N), capsular wall (CW) and peripheral extracapsulum containing digestive vacuoles (DV) and algal symbionts in perialgal vacuoles (PV). The skeletal matter (SK) is enclosed within the cytokalymma, an extension of the cytoplasm, that acts as a living mold to dictate the shape of the siliceous skeleton deposited within it. Reproduced with permission from Anderson OR (1983) *Radiolaria*. New York: Springer-Verlag.

is not simply a consequence of passive physical chemical processes taking place at interfaces among the frothy components of the cytoplasm as was previously proposed by some researchers.

Taxonomy

Radiolarians are included in some modern classification schemes in the kingdom Protista. However, the category of radiolaria as such is considered an artificial grouping. Instead of the group 'Radiolaria', two major subgroups previously included in 'Radiolaria' are placed in the kingdom Protista. These are the Polycystina and the Phaeodaria. Polycystina are radiolarians that contain a central capsule with pores that are rather uniform in shape and either uniformly distributed across the surface of capsular wall, or grouped at one location. The Phaeodaria have capsular walls with two distinctive types of openings. One is much larger and is known as the astropyle with an elaborately organized mass of cytoplasm extending into the extracapsulum. The other type is composed of smaller pores known as parapylae with thin strands of emergent cytoplasm. Some Phaeodaria also have skeletons that are enriched in organic matter compared with the skeletons of the Polycystina. Among the Polycystina, there are two major taxonomic groups, the Spumellaria and Nassellaria, assigned as orders in some taxonomic schemes. Spumellaria have central capsules that are usually spherical or nearly so at some stage of development and have pores distributed uniformly over the entire surface of the capsular wall. All known colonial species are members of the Spumellaria. Although expert opinion varies, there are two families and about 10 genera of colonial radiolarians. There are seven widely recognized families of solitary Spumellaria with scores of genera. Nassellaria have central capsules that are more ovate or elongated and the fusules are located only at one pole of the elongated capsular wall. This pore field is called a porochora and the fusules tend to be robust with axopodia that emerge through outward-directed collar-like thickenings surrounding the pore rim. Moreover, the skeleton of the Nassellaria, when present, tends to be elongated and forms a helmet-shaped structure, often with an internal set of rods forming a tripod to which the external skeleton is attached. Current systematics include seven major families with numerous genera. Spumellarian skeletons are typically more spherical, or based on a form that is not derived from a basic tripodal or helmet-like architectural plan. The shells of the Phaeodaria are varied in shape. Some species have ornately decorated open lattices resembling geodesic structures composed of interconnected, hollow tubes of silica. Other species have thickened skeletons resembling small clam shells with closely spaced pores on the surface. There are 17 major families with scores of genera. Since many species of radiolarians were first identified from sediments based solely on their mineralized skeletons, much of the key taxonomic characteristics include skeletal morphology. Increasingly, evidence of cytoplasmic fine structure obtained by electron microscopy and molecular genetic analyses is being used to augment skeletal morphology in making species discriminations and constructing more natural evolutionary relationships. It is estimated that there are several hundred valid living species of radiolarians.

Biomineralization

Biomineralization is a biological process of secreting mineral matter as a skeleton or other hardened product. The skeleton of radiolaria is composed of hydrated opal, an oxidized compound of silicon (nominally $SiO_2 \cdot nH_2O$) highly polymerized to form a space-filling, glassy mass incorporating a variable number (n) of water molecules within the molecular structure of the solid. Electron microscopic evidence indicates that some organic matter is incorporated in the skeleton during early stages of deposition, but on the whole, the skeleton is composed mostly of pure silica. Electron microscopic, X-ray dispersive analysis shows that a small amount of divalent cations such as Ca^{2+} may be incorporated in the final veneer deposited on the surface to enhance the hardness of the skeleton. During deposition of the skeleton, the cytoplasm forms the living cytokalymma, i.e., the cytoplasmic silica-depositing mold, by extension of the surface of the rhizopodia. The cytokalymma enlarges as silica is deposited within it, gradually assuming a final form that dictates the morphology of the internally secreted skeleton. Small vesicles are observed streaming outward from the cell body into the cytoplasm of the cytokalymma and these may bring silica to be deposited within the skeletal spaces inside the cytokalymma. The cytoplasmic membrane surrounding the developing skeleton appears to act as a silicalemma or active membrane that deposits the molecular silica into the skeletal space. During deposition, the dynamic molding process is clearly evident as the living cytoplasm continuously undergoes transformations in form, gradually approximating the ultimate geometry of the species-specific skeleton being deposited by the radiolarian cell. In general, species with multiple, concentric, lattice shells surrounding the central capsule appear to lay down the lattices successively, progressing outward from the innermost shell.

The process of skeletal construction has been documented in fair detail for a few species, most notably among the colonial radiolaria. Two forms of growth have been identified. Bar growth is a process of depositing silica as rodlets within a thin tubular network of cytoplasm formed by the cytokalymma. The rodlets become connected during silicogenesis and further augmented with silica to form a porous lattice with typically large polygonal pores. The pores, once formed, may be further subdivided into smaller pores by additional bar growth that spans the opening of the pore. Rim growth occurs by deposition of silica as curved plates that are differentially deposited at places to form rounded pores. At maturity, these are typically spherical skeletons with rather regular, rounded pores scattered across the surface. For both types of skeletons, in some species, the ratio of the bar width between the pores to the pore diameter is a taxonomic diagnostic feature.

The rate of silica biomineralization in some species has been determined by daily observation of growth of individuals in laboratory culture using light microscopy. The amount of silica in the skeleton of a living radiolarian is mathematically related to the size of the skeleton. For example, in the spumellarian species *Spongaster tetras* with a rectangular, spongiose skeleton, the amount of silica (W) in micrograms (μg) as related to the length of the major diagonal axis of the quadrangular shell (L) in micrometers (μm) is approximated as follows:

$$W = \left(3.338 \times 10^{-6}\right) \cdot L^{2.205} \qquad [1]$$

The average daily growth in cultures of an *S. tetras* is 3 μm with an average daily gain in weight of *c.* 8 ng. The total weight gain for one individual radiolarian during maturation is about 0.1 μg. Silica deposition during maturation appears to be sporadic and irregular, varying from one individual to another, with periods of rapid deposition followed by plateaus in growth. The amount of skeletal opal produced by *S. tetras* alone in the Caribbean Sea, for example, is *c.* 42 μg per m^3 of sea water, with a range of 8–61 μg per m^3. Peak production occurred in mid-summer (June to July). The rate of total radiolarian-produced biogenic opal settling into the ocean sediments at varying oceanic locations has been estimated in the range of 1–10 mg per m^2 per day.

Reproduction

Protozoa reproduce by either asexual or sexual reproduction. Asexual reproduction occurs by cell division during mitosis to produce two or more genetically identical offspring. Sexual reproduction occurs by the release of haploid gametes (e.g., sperm and egg cells) that fuse to produce a zygote with genetic characteristics contributed by both of the parent organisms. Thus, sexual reproduction permits new combinations of genetic material and the offspring are usually genetically different from the parents. There is evidence that some colonial radiolaria have asexual reproduction. The central capsules within the colony have been observed to divide by fission. This increases the number of central capsules and allows the colony to grow in size. The colony may also break into parts, thus increasing the total numbers of colonies at a given location. In most species of radiolaria, reproduction occurs by release of numerous flagellated swarmer cells that are believed to be gametes. The nucleus of the parent radiolarian undergoes multiple division and the entire mass of the parent cell is converted into uninucleated flagellated swarmers. These are released nearly simultaneously in a burst of activity, and presumably after dispersal fuse to form a zygote. The details of gamete fusion and the early ontogenetic development of radiolaria are poorly understood and require additional investigation. Ontogenetic development of individuals from very early stages to maturity has been documented in laboratory cultures and the stages of skeletal deposition are well understood for several species, as explained above in the section on biomineralization.

Physiological Ecology and Zoogeography

The physiological ecology of radiolaria has been studied by collecting samples of radiolaria and other biota at varying geographical locations in the world oceans to determine what abiotic and biotic factors are correlated with and predict their abundances, and by experimental studies of the physical and biological factors that promote reproduction, growth, and survival of different species under carefully controlled laboratory conditions. Temperature appears to be a major variable in determining abundances of some species of radiolaria. For example, high latitude species that occur abundantly at the North or South Poles are also found at increasing depths in the oceans toward the equator. Since the water temperature in general decreases with depth, these organisms populate broad depth regions within the water column that match their physiological requirements. Species that occur in subtropical locations, where the water is intermediate in temperature based on a global range, are found at the equator at intermediate water depths that are cooler than the warm surface water. Some species are characteristically most abundant in only warm, highly productive water masses. For example, some species of colonial radiolaria occur typically in surface water near the equator in the Atlantic Ocean, while others are most abundant at higher latitudes in the Sargasso Sea where usually the water is also less productive. Upwelling regions where deep, nutrient-enriched sea water is brought to the surface are typically highly productive regions for radiolaria, as occurs for example along the Arabian, Chilean, and California coast lines. Shallow-water dwelling species have been categorized into seven zoogeographic zones based on water mass properties: (1) SubArctic at high northern latitudes; (2) transition region as occurs in the North Pacific drift waters; (3) north central region, typical of waters within the large anticyclonic circulation of the North Pacific; (4) equatorial region in locations occupied by the North and South Equatorial Current systems; (5) south central water mass, as in the South Pacific anticyclonic circulation pattern; (6) subAntarctic, a water regime bounded on the north by the Subtropical Convergence and on the south by the Polar Convergence; and (7) Antarctic, bounded by the Polar Convergence on the north and the Antarctic Continent on the south.

The growth requirements of some species have been studied extensively in laboratory cultures. For example, the following three surface- to near-surface-dwelling species exhibit a range of optimal growth conditions. *Didymocyrtis tetrathalamus*, with a somewhat hourglass-shaped skeleton (150 μm), prefers cooler water (21–27°C) and salinities in the range of 30–35 ppm. *Dictyocoryne truncatum*, a spongiose triangular-shaped species (300 μm), is more intermediate in habitat requirements with optimal temperature of 28°C and salinity of 35 ppm. *Spongaster tetras*, a quadrangular, spongiose species (300 μm), prefers warmer, more saline water (*c.* 28°C and 35–40 ppm). The temperature tolerance ranges (in °C) for the three species also show a similar pattern of increasing preference for warmer water, i.e., 10–34, 15–28, and 21–31, respectively.

The prey consumed by radiolarians varies substantially among species, but many of the polycystine species appear to be omnivorous, consuming both phytoplankton and zooplankton prey. The smaller species consume microplankton and bacteria. Larger species are capable of capturing copepods and small invertebrates. Phaeodaria, especially those species dwelling at great depths in the water column, appear to consume detrital matter in addition to preying on plankton in the water column. The broad range of prey accepted by many of the radiolarians studied thus far suggests that they are opportunistic feeders and are capable of adapting to a broad range of trophic conditions.

The role of algal symbionts, when present, has been debated for some time – beginning with their discovery in the mid-nineteenth century. At first, it was supposed that the green symbionts may largely provide oxygen to the host. However, most radiolaria dwell in fairly well-oxygenated habitats and it is unlikely that photosynthetically derived oxygen is necessary. The other competing hypothesis was that the symbionts provide organic nourishment to the host. Modern physiological studies have confirmed that the algal symbionts provide photosynthetically produced nutrition for the host. Biochemical analyses combined with ^{14}C isotopic tracer studies have shown that stores of lipids (fats) and carbohydrates in the host cytoplasm contain carbon derived from algal photosynthetic activity. Well-illuminated, laboratory cultures of symbiont-bearing radiolaria survive for weeks without addition of prey organisms. Some of the algal symbionts are digested as food and can be replaced by asexual reproduction of the algae, but it appears that much of the nutrition of the host comes from organic nutrients secreted into the host cytoplasm by the algal symbionts. This readily available, 'internal' supply of autotrophic nutrition makes symbiont-bearing radiolaria much less dependent on external food sources and may account in part for their widespread geographic distribution, including some oligotrophic water masses such as the Sargasso Sea.

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PROTOZOA, PLANKTONIC FORAMINIFERA

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Introduction

Planktonic foraminifers are single celled organisms (protozoans) sheltered by a test (shell) made of calcite, with an average test diameter of 0.25 mm. They live in surface waters of all modern open oceans and deep marginal seas, e.g., Mediterranean, Caribbean Sea, Red Sea, and Japan Sea, and are almost absent from shelf areas including the North Sea and other shallow marginal seas. Planktonic foraminifers constitute a minor portion of the total zooplankton, but are the main producers of marine calcareous particles deposited on the ocean floor and form the so-called 'Globigerina ooze.'

Planktonic foraminifers (Greek: foramen = opening, ferre = carry) first appeared in the middle Jurassic, about 170 million years ago (Ma), and spread since the mid-Cretaceous over all world oceans. Times of main appearance of new species in the Aptian (120 Ma), the Turonian (90 Ma), the Paleocene (55 Ma), and the Miocene (20 Ma), alternate with phases of main extinction in the Cenomanian (95 Ma), at the Cretaceous/Tertiary boundary (60 Ma), and in the Upper Eocene (40 Ma). Modern planktonic foraminifers have evolved since the early Tertiary, when first spinose species occurred directly after the Cretaceous/Tertiary boundary. Approximately 450 fossil and 50 Recent species are known, not including species based on molecular biology investigations. The appearance and radiation of new species seem to correlate with the development of new realms and niches, linked to plate tectonics and paleoceanographic changes. The geographical distribution and main events in planktonic foraminiferal evolution are associated in general with water mass properties, e.g., availability of food or temperature. The reproductive strategies depend highly on their life habitat in the photic zone or slightly below. The life span of planktonic foraminifers varies between 14 days and a year, mostly linked to the lunar cycle. Most living species bear symbionts requiring a habitat in the upper to middle photic zone. Their feeding habit depends on the spinosity (spinose versus nonspinose species) in respect to the size and class of prey. Predators that are specialized on planktonic foraminifers are not known.

History

With the technological improvement of microscopes d'Orbigny in 1826 was able to describe the first planktonic foraminiferal species, *Globigerina bulloides*, from beach sands, and classified it as a cephalopod. In 1867 Owen described the planktonic life habit of these organisms. Following the Challenger Expedition (1872–1876) the surface-dwelling habitat of planktonic foraminifers was recognized. Rhumbler first described the biology of foraminifers in 1911. In the first half of the twentieth century, foraminifers were widely used for stratigraphic purposes, and many descriptions were published, mainly by Josef A. Cushman and co-workers. Studies on the geographic distribution of individual foraminiferal species are based on samples from the living plankton since the work of Schott in 1935. Planktonic foraminifers have been used since the beginning of the twentieth century to date marine sediments drilled by oil companies, and later on through the Deep-Sea Drilling and Ocean Drilling Programs. In addition, extensive studies on distribution, ecology of live and fossil faunas were carried out to understand the changing marine environment. The ecological significance has been applied in paleoecological and paleoceanographic settings and yielded subtle information on ancient oceans and the Earth's climate. Recent investigation still focuses on evolution and population dynamics. Modern techniques, e.g., polymerase chain reaction (PCR), are being used to reveal the genetic code, and their relation to morphological classification tests needs to be checked.

Methods

Planktonic foraminifers are sampled from the water column by plankton nets of various design, with a mesh size of 0.063–0.2 mm, by employing plankton recorders, water samplers, pumping systems, or collection by SCUBA divers. To study faunas from sediment samples or consolidated rock, the surrounding sediment has to be disaggregated by hydrogen peroxide, tensids, acetic acid (pure), or physical methods, and washed over a sieve (0.03–0.063 mm). Shells may be studied under a binocular microscope, or with a scanning electron microscope