BACTERIAL CONTAMINATION

See **VIRAL AND BACTERIAL CONTAMINATION OF BEACHES**

BACTERIOPLANKTON

H. W. Ducklow, The College of William and Mary, Gloucester Point, VA, USA

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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 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 DOM has a turnover time of centuries to millennia, and seems to become labile (vulnerable to bacterial attack) when the ocean thermohaline circulation returns

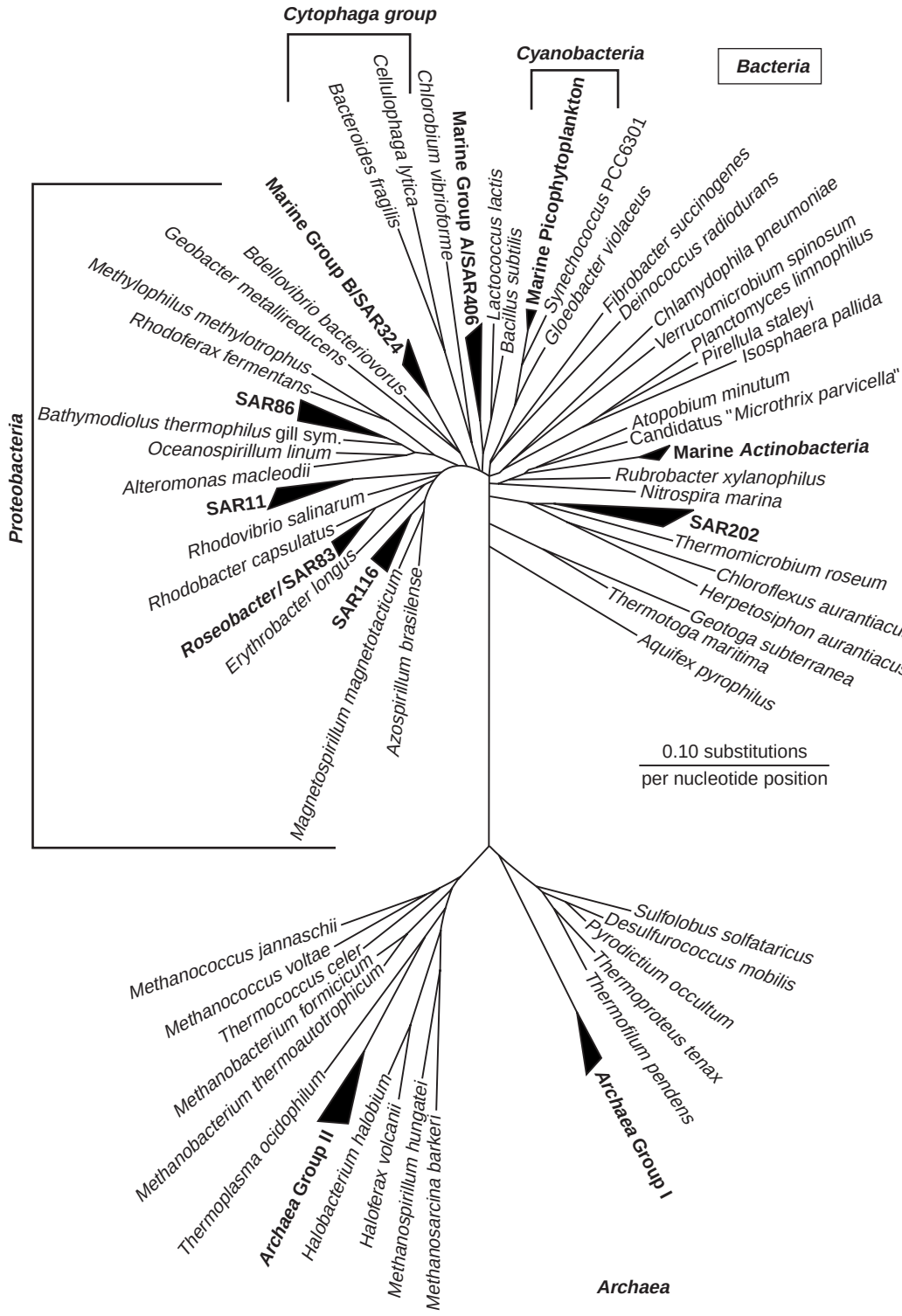

Figure 1 Dendrogram showing relationships among the most widespread SSU rRNA gene clusters among the marine prokaryotes (the 'bacterioplankton'). (Modified after Giovannoni SJ, in Kirchman (2000).)

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

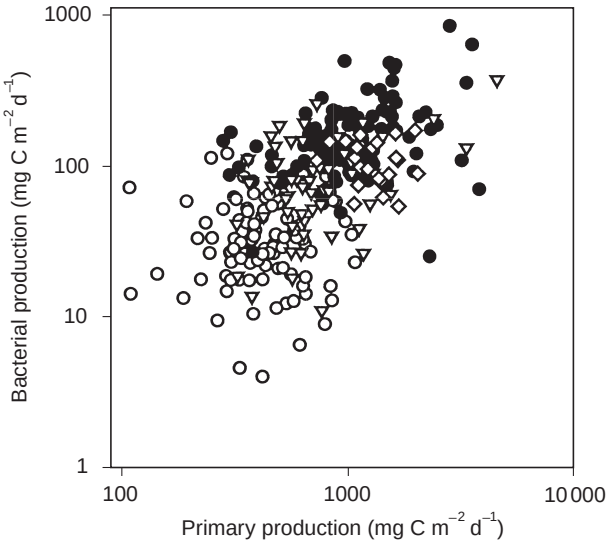

Figure 2 Bacterial production plotted against primary production for the euphotic zone in several major ocean regimes or provinces. The overall data set has a significant regression, but the individual regions do not. ○, Sargasso Sea; ●, Arabian Sea; ◇, equatorial Pacific; ▽, equatorial Pacific.

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 nmol l^{-1}, termed oligotrophs, cannot survive when DOM is greater than about 0.1–1 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 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.

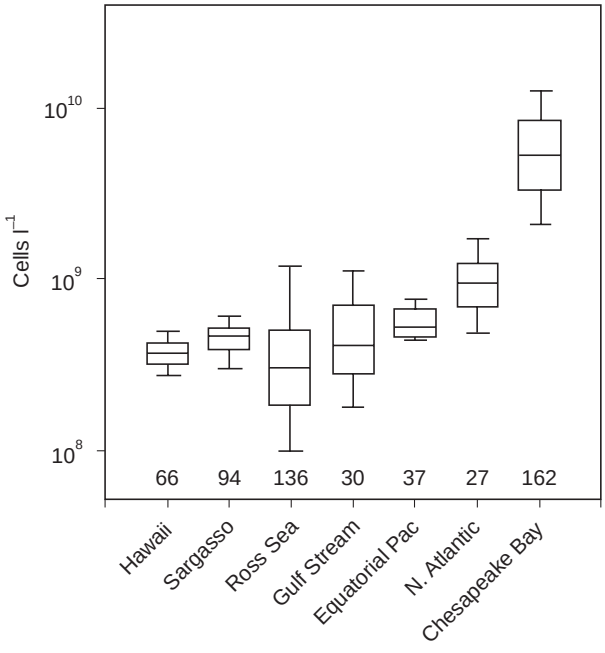

Figure 3 Bacterial abundance in the euphotic zone of several major ocean provinces. The box plots show the median, 10th, 25th, 75th and 90th centiles of the data. The number of samples is listed for each region. There is no statistical difference among the regions except for Chesapeake Bay.

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 $7–15 \times 10^{-15}$ g C cell^{-1} for oceanic cells and $15–25 \times 10^{-15}$ 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.

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 $4–8 \times 10^9$ 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

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).

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**). 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 (BCD = BR + 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 μm 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

Carbon Cycle. Copepods. Hydrothermal Vent Deposits. Hydrothermal Vent Fauna, Physiology of. Marine Mammal Trophic Levels and Interactions. Microbial Loops. Network Analysis of Food Webs. Primary Production Methods. Primary Production Processes. Protozoa, Planktonic Foraminifera. Protozoa, Radiolarians. Small-scale Physical Processes and Plankton Biology.

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BALEEN WHALES

J. L. Bannister, The Western Australian Museum, Perth, Western Australia

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Diagnostic Characters and Taxonomy

Baleen or whalebone whales (Mysticeti) comprise one of the two recent (nonfossil) cetacean suborders. They differ from the other suborder (toothed whales, Odontoceti), particularly in their lack of functional teeth. Instead they feed on relatively very small marine organisms by means of a highly specialized filter-feeding apparatus made up of baleen plates 'whalebone' attached to the gum of the upper jaw. Other differences from toothed whales include the baleen whales' paired blowhole, symmetrical skull, and absence of ribs articulating with the sternum.

Baleen whales are generally huge. In the blue whale they include the largest known animal, growing to more than 30 m long and weighing more than 170 tonnes. Like all other cetaceans, baleen whales are totally aquatic. Like most of the toothed whales, they are all marine. Many undertake very long migrations, and some are fast swimming. A few species come close to the coast at some part of their life cycle and may be seen from shore; however, much of their lives is spent remote from land in the deep oceans. Baleen whale females grow slightly larger than the males. Animals of the same species tend to be larger in the Southern than in the Northern Hemisphere.

Within the mysticetes are four families: right whales (Balaenidae, balaenids), pygmy right whales (Neobalaenidae, neobalaenids), gray whales (Eschrichtiidae, eschrichtiids); and 'rorquals' (Balaenopteridae, balaenopterids). Within the suborder, 12 species are now generally recognized (**Table 1**).

Right whales are distinguished from the other three families by their long and narrow baleen plates and arched upper jaw. Other balaenid features include, externally, a disproportionately large head (*c.* one-third of the body length), long thin rostrum, and huge bowed lower lips; they lack multiple ventral grooves. Internally, there is no coronoid process on the lower jaw and cervical vertebrae are fused together. Within the family are two distinct groups: the bowhead (*Balaena mysticetus*) of northern polar waters (formerly known as the 'Greenland' right whale) and the three 'black' right whales (*Eubalaena* spp.) of more temperate seas (so called to distinguish them from the 'Greenland' right whale) (**Figure 1**). All balaenids are robust.

Pygmy right whales (*Capnea marginata*) have some features of both right whales and balaenopterids. The head is short (*c.* one-quarter of the body length), although with an arched upper jaw and bowed lower lips, and there is a dorsal fin. The relatively long and narrow baleen plates are yellowish-white, with a dark outer border, quite different from the all-black balaenid baleen plates. Internally, pygmy right whales have numerous broadened and flattened ribs.

Gray whales (*Eschrichtius robustus*) are also somewhat intermediate in appearance between right whales and balaenopterids. They have short narrow heads, a slightly arched rostrum, and between two and five deep creases on the throat instead of the balaenopterid ventral grooves. There is no dorsal fin, but a series of 6 to 12 small 'knuckles' along the tail stock. The yellowish-white baleen plates are relatively small.

Balaenopterids comprise the five whales of the genus *Balaenoptera* (blue, *B. musculus*; fin, *B. physalus*; sei, *B. borealis*; Bryde's, and minke, *B. acutorostrata* & *B. bonaerensis*; whales and the humpback whale (*Megaptera novaeangliae*). All