

# The Microbial Loop

BY LAWRENCE R. POMEROY, PETER J. IeB. WILLIAMS, FAROOQ AZAM, AND JOHN E. HOBBIE

*I presume that the numerous lower pelagic animals persist on the infusoria, which are known to abound in the open ocean: but on what, in the clear blue water, do these infusoria subsist?*

— Charles Darwin (1845)

Answering Charles Darwin's prescient question has taken us nearly two centuries. Only in recent decades have methods and concepts been developed to explore the significance of microbes in the ocean's web of life. Bacteria in aquatic ecosystems were first recognized for their role in the decomposition of organic material and the remineralization of inorganic nutrients, a role that only became fully accepted in the 1980s. Their importance as photosynthetic producers of organic matter became evident when so-called blue-green algae were acknowledged as being bacteria, and the microscopic cyanobacterium of the genus *Synechococcus* was discovered to be abundant in the oceans—particularly

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in the vast oligotrophic blue water where they are the dominant autotrophs.

We now know that every liter of “clear blue water” is teeming with a billion microbes—bacteria, viruses, and protists—far exceeding all multi-cellular metazoa in abundance, biomass, metabolic activity, and genetic and biochemical diversity. Their struggle for survival is manifest in a web of microbial life, the microbial loop, which is functionally intertwined with the more familiar food web of plants, herbivores, and carnivores. It channels energy and carbon via bacteria to protozoa (Darwin's infusoria), to larger zooplankton such as copepods and krill, and on to fishes and cetaceans. Indeed, when we eat mahi-mahi, we are the top predator in a food web that has some of its beginnings in the microbial loop.

About one-half of the oxygen in every breath we take derives from photosynthetic bacteria within the marine microbial loop. Bacteria manage to populate all parts of the ocean by capturing nutrients and energy from diverse sources. Photosynthetic bacteria carry out much of the primary production of organic matter in the central ocean basins. Heterotrophic bacteria capture dis-

solved organic molecules from seawater as well as organic particles that they “digest” with enzymes. Some bacteria and archaea oxidize inorganic chemicals for energy, and the carbon they fix into organic matter serves as basis for food webs in diverse ecosystems, including some in seemingly uninhabitable environments. The “smoke” coming from hot vents on the seafloor may even contain some bacteria and archaea (Box 1). Earth's ocean is most certainly a sea of microbes; without them it would be a very different place, less hospitable to all life. Indeed, without the activity of these organisms, the cycles of Nature would very quickly come to a halt. This is not the case for higher organisms: whereas the near extinction of the great whales by fishing undoubtedly modified the ecology of the Antarctic, it certainly did not bring it to a stop.

## MICROBIAL DOMINANCE

Earth's ocean is estimated to contain  $10^{29}$  bacteria (Whitman et al., 1998), a number larger than the estimated  $10^{21}$  stars in the universe. Their great numerical abundance makes up for their size, typically 0.2–0.6  $\mu\text{m}$  in diameter. The total mass of bacteria in the ocean

exceeds the combined mass of zooplankton and fishes. Fish biomass is too small even to show relative to others in Figure 1. The entire microbial food web, including protozoan microzooplankton, is typically some five to ten times the mass of all multicellular marine organisms (locally, these ratios vary widely). The potential metabolic dominance of microorganisms is even greater than their biomass would suggest (Figure 2).

Heterotrophic bacteria have potentially fierce metabolic rates. For example, the marine bacterium *Pseudomonas natrigens* (now renamed *Beneckea natrigens*) can, under optimum conditions, divide with a frequency of < 10 min per division, a growth potential related to its surface-to-volume ratio. Whereas biomass (i.e., volume) sets the ultimate potential for metabolism and therefore growth, all organic and inorganic nutrients, oxygen, and waste products have to pass through the cell surface. Thus, the metabolism per unit biomass is controlled by the surface-to-volume relationship. In the case of a simple sphere, this would be  $4\pi r^2 / (4/3)r^3 = 3/r$ . In this simple instance, the metabolic rate is inversely proportional to the linear rela-

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tionship between size and metabolism that in part gives rise to the allometric relationship known as the “mouse to the elephant” curve. Taken literally,

### BOX 1. THE KINDS OF MICROORGANISMS

Microorganisms include members of many branches of the tree of life, from the most primitive to the most advanced. What were once simply called “bacteria” have been separated into two distinct domains, Bacteria and Archaea, initially on the basis of differences in their ribosomal RNA (Woese and Fox, 1977). Archaea look superficially much like bacteria, but their basic biochemistry is very different, in some ways more like that of higher organisms (Domain Eukarya), while in other ways it is unique. This is reflected in their position on the Tree of Life. Some archaea are “extremophiles,” living in very hot water and environments that are very salty, acidic, or alkaline. Others live in extreme cold, in anaerobic mud, or in our anaerobic gut, where they outnumber the living cells in our bodies. Protozoa (flagellates and ciliates) and fungi are in the Domain Eukarya along with animals and most of what we call plants.

a bacterium the size of a micrometer would have a metabolic rate a million times greater than a human. Other factors—for example, the rate of DNA replication, convoluted surfaces such as lungs and gills, the availability of growth substrates—ameliorate the discrepancy somewhat, so that in the case of a human

watts per gram dry weight. Put in more understandable terms, a mass of *B. natrigens* equal to 100 humans would have an energy throughput of about a gigawatt, much the same as a nuclear power station. This metabolic potential under optimal circumstances would be rarely, if ever, achieved in nature for a number of reasons, notably the low concentration of organic nutrients; but, in principle, it gives bacteria the potential for very rapid response to favorable conditions. This is important ecologically in the oceans, for if the valuable inorganic nutrients present in particulate organic material produced by plankton are to remain in surface waters and not lost to the ocean depths, there must be rapid colonization and decomposition of these particles. It may be significant that the bacterium that holds the gold medal for growth rate

versus this particular bacterium, the discrepancy is still about 100,000 fold. The energy throughput of *B. natrigens* dividing every 10 minutes would be 2 kilo-

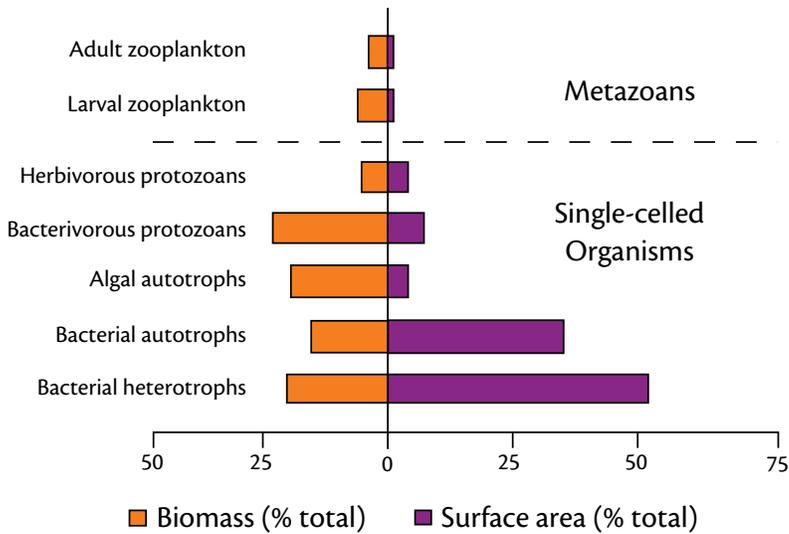


Figure 1. Distribution of biomass and calculated surface area (expressed as a percentage of total) for planktonic trophic groups in the euphotic zone of the oceans. The biomass value is a geometric mean of the data from various oceanic areas; surface area is calculated assuming simple spherical geometry. The total biomass for the plankton is  $50 \text{ mg C m}^{-3}$  and the total surface area is  $1.2 \text{ m}^2 \text{ m}^{-3}$ . Megaplankton, such as medusae, have not been included, although this would not materially change the picture. Compiled from Ducklow (1999), Pomeroy (2004), and Robinson and Williams (2005)

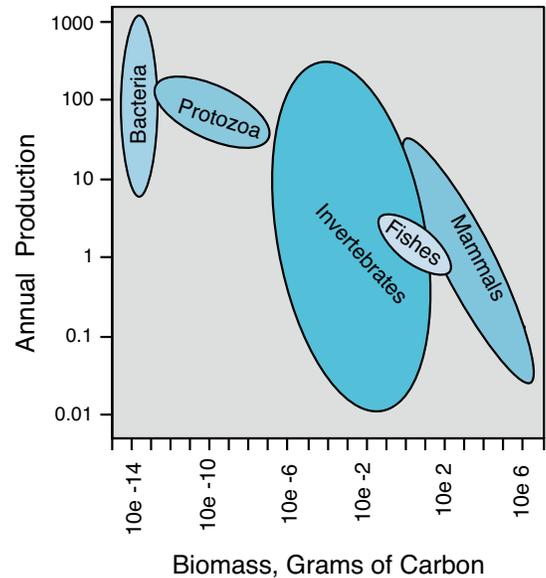


Figure 2. Comparison of the production of living organic matter per unit of biomass by different kinds and sizes of organisms showing the relatively high productivity per unit weight by microorganisms. Modified from Pomeroy (2001)

is a marine, rather than a soil, isolate.

Although we usually consider numbers and biomass as the significant parameters of food webs, Figure 1 suggests that surface area also provides valuable insights. What is striking is the overwhelming surface area associated with bacteria. If surface area is taken as a proxy for metabolism, this figure gives a simple illustration of the metabolic importance of bacteria in the oceans, and it brings home the fact that the oceans are a microbial world, not a pond of fishes, dolphins, and whales. Enzymes bound to those living bacterial surfaces break down complex and even quite refractory organic materials—lignin, cellulose, chitin, and petroleum—into smaller, simpler molecules that can be absorbed and utilized by bacteria. External digestive processes provide shared benefits for motile bacteria, which

have been called the “ultimate swimming stomachs” (Azam, 1998). Most of the organic matter available to consumers in the ocean is used and respired by bacteria (Robinson and Williams, 2005). Many bacteria use flagellar motility to locate and attach to organic particles where fast-growing cells digest all or part of the particle, releasing dissolved organic molecules into the water to be utilized by the microbial community (Azam, 1998).

Bacteria and archaea also are the ultimate survivors, living even in geologically old rock formations (Lin et al., 2006). They possess a metabolic gearshift that only a few multicellular organisms, such as bears and hummingbirds, possess. Unlike birds and beasts, bacteria alter not only their metabolic rate but also their morphology. Resting cells are small, with minimal water con-

tent. Bacteria do not have a set period of quiescence, but just keep sampling their environment. When good times happen, resting cells rapidly enlarge and mobilize enzymes.

Because they are a large fraction of the biomass and, when active, have relatively high metabolic rates, microorganisms dominate the flux of energy and biologically important chemical elements in the ocean. Photosynthetic bacteria often are the dominant producers of new organic matter in central ocean basins (Figure 3). Archaea also extract energy from reduced chemical compounds present in the water, such as methane, hydrogen sulfide, or ammonium. For individual bacteria, their world consists, more or less, of the cubic meter of seawater in which they reside. Each cubic meter contains a diverse community of microbial residents and is visited peri-

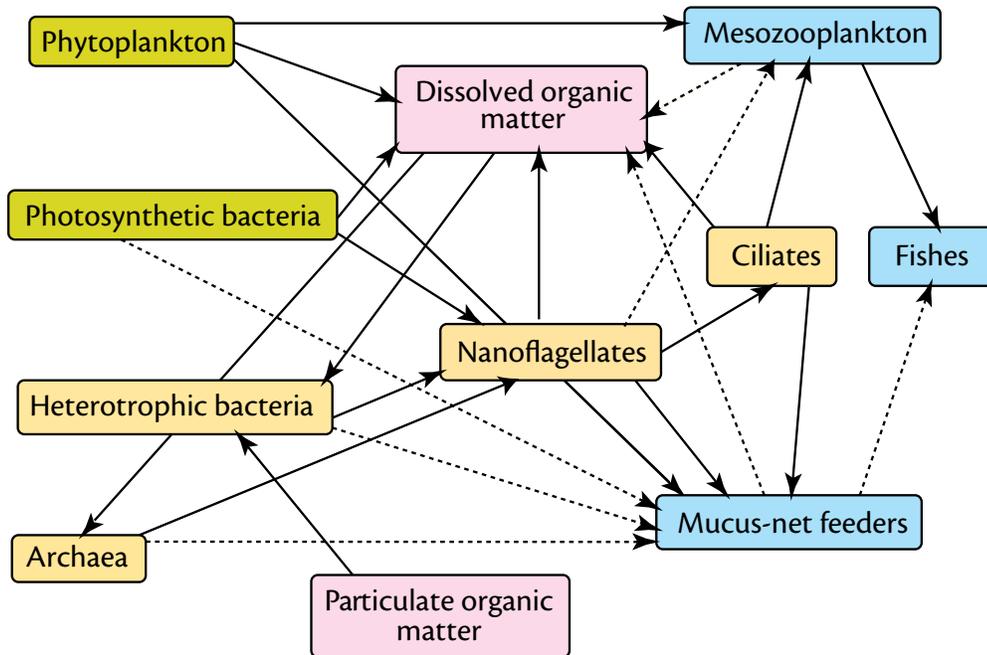


Figure 3. Simplified diagram of the ocean's food web showing the dominant roles of the microbial loop. The major fluxes of carbon and energy are delineated by continuous lines; fluxes usually of lesser magnitude are delineated by broken lines. Mucus-net feeders (salps and other microphages) are separated from other mesozooplankton because of their different feeding mode. Other than the mesozooplankton (including mucus-net feeders) and fishes (all blue boxes), the boxes represent organisms that are a part of the microbial loop (green = photosynthetic and yellow = heterotrophic).

odically by large swimming or falling organisms, fecal particles, and microscopic aggregates composed of all of the organic and inorganic particulate material in seawater.

### ROLES IN THE FOOD WEB

Microorganisms are capable of creating a sustained cycle of production and decomposition of organic matter, requiring only the input of sunlight or the chemicals released from rivers and from hot vents that occur near undersea volcanism. Phytoplankton and photosynthetic and chemosynthetic bacterioplankton convert carbon dioxide or bicarbonate and inorganic nitrogen and phosphorus into the organic constituents of their cells. Microflagellates eat heterotrophic and the smaller autotrophic bacteria. In so doing, they usually control the numbers of bacteria in the sea, and are

consumed in turn by larger ciliated protozoa. Ciliates are a staple food of copepods and other mesozooplankton that are the food of larval fishes (Figure 3). On the scale of micrometers, at which many processes of the microbial loop occur, bacteria and protozoans are swimming in water on a scale (so-called low Reynolds number) where the physics associated with movement is very different from that which we experience. It is

ously does not change with size; it is more about momentum or actually the lack of it. A better analogy is the rapid attenuation of movement of balloons thrown in the air. A rapidly swimming bacterium will coast for a mere hydrogen bond length once it stops propelling itself—a deceleration force many times greater than driving a Formula I Grand Prix racing car at full speed into a wall of granite. Our intuitions, derived from

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often commented that on the microbial scale, the system behaves as if the water had a viscosity of honey. The analogy is prone to be misleading as viscosity obvi-

the scale we live in, serve us poorly when thinking about the microbial world.

Traditionally, scientists viewed the microbial food web as primarily a site

of remineralization, supplying nitrogen and phosphorus for use as nutrients by phytoplankton. Indeed, this is one of its important functions. However, assimilation of inorganic elements into organic matter by archaea and photosynthetic bacteria and its transfer via protozoans

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to metazoans is also significant, even though the multiple transfers of organic matter that occur in blue-water food webs greatly reduce the efficiency of transfer to terminal consumers. In the blue water, where most phytoplankton are small and photosynthetic bacteria are often the dominant primary producers of organic matter, only 1–2% of the primary production may be assimilated finally by fishes (Ducklow et al., 1986). That this food web supports fishes at all is a result of the versatility of the bacterial community in using many sources of nutrients and its rapid response to new sources.

Most of the time, in most of the ocean, bacteria in the active mode are growing and dividing at a slow pace, circa 0.2 times per day, using often-meager local sources of nutrients. Virtually fixed in place in the water, they await a helpful event. A passing zooplankton may relieve itself, leaving a trail of dissolved and particulate organic matter in the water. A copepod's fecal pellet, or smaller microscopic particles that have stuck together to form an aggregate,

may fall slowly through that meter-sized community. In passing, the particle accumulates bacteria that attach, morph into larger cells, mobilize enzymes, and begin to digest the particle while multiplying (2 times per day) in numbers (Azam et al., 1993). Some of the daughter cells

may later depart the particle as it disintegrates (Jacobsen and Azam, 1984). The largest, heaviest fecal pellets fall into the depths of the ocean before being utilized as completely as possible by embedded bacteria, but the majority, even in polar waters, disintegrate in the upper 50–100 meters (LeFèvre et al., 1998).

#### MICROBIAL NATURAL HISTORY

How do we know about bacterial and protozoan behavior that takes place on a microscopic scale in the sea? This is really natural history, a kind of observational investigation that has been done relatively easily with birds and beasts for centuries. Describing the activities of microorganisms in the ocean, on a microscopic scale, presents new challenges, however. On that scale (as on others), the ocean is not completely or continuously mixed. Just as there are microhabitats in a forest, nano- and pico-habitats occur in ocean water (Azam, 1998). The natural history of the microbial loop is still to some extent inferential, based on an understanding of the physics and chemistry, as well as

the microbiology, of the system. We cannot sit and watch events as would the ornithologist in the forest. Simulation models have been helpful in bringing together quantitatively the rate of fall of fecal particles and aggregates, diffusion rates of dissolved materials in the water, and swimming speeds of copepods and motile bacteria to achieve a virtual description of the natural history. Interactive work with computing simulations and experiments, often aboard ships, that use a variety of chemical and radioactive tracers, cell sorters, and microscopes has helped us to refine our understanding of processes that occur on scales of less than a cubic centimeter in the ocean. However, our attempts to depict for this article the distribution of bacteria and other organisms in a cartoon of a typical microliter or nanoliter of water failed, because the space is 99.99999% water. This is not the rain forest.

Bacteria and archaea are everywhere, albeit with major differences in activity rates and lifestyles. Within these groups are many specialists with suites of enzymes for specific tasks. Much research has gone into understanding the differences among polar, temperate, and tropical regions, places of high versus low photosynthetic production, and between surface waters and abyssal waters that are dark, relatively cold, and with sparse and patchy sources of nutrition. These microbial communities have persisted since the early history of the planet. A billion or more years ago, the microbial loop became a self-sustaining community of organisms. It now interacts with the lesser mass of large, multicellular organisms of the ocean in

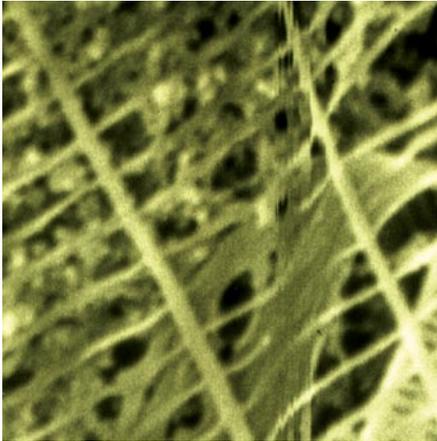


Figure 4. Mucus net of a salp with material behind it that has been collected on the net. Dimensions of the openings in the net are  $0.2 \times 2$  micrometers, permitting capture of microorganisms. *Electron-micrograph by Shirley F. Nishino*

significant ways, but the larger part of all energy captured by marine photosynthesis, by both bacteria and plants, is consumed ultimately by microorganisms (Ducklow et al., 1986; del Giorgio and Williams, 2005). Although the ocean contains a large volume of dissolved organic matter too refractory for bacteria to process, some of it thousands of years old, it is an extremely small fraction of what has been produced over mil-

lions of years. Microorganisms process nearly everything, from a microscopic aggregate of organic detritus to a whale carcass on the bottom.

Not all energy, carbon, nitrogen,

and phosphorus pass through the long, multistep microbial food web. Some of it is short-circuited by organisms called microphages. They are salps, appendicularians, and some crustacean plankton, for example, krill, which are able to filter the protozoans and some of the bacteria from the water. Salps and doliolids (prochordates) feed by pumping seawater through a fine mucus net that they secrete and ingest, along with bacteria, protozoans, and phytoplankton caught on the net (Figure 4). Some of the pterapods (planktonic mollusks) cast mucus nets in the water to which microorganisms adhere. These are the most direct and efficient paths for energy from microbes to larger organisms (LeFèvre et al., 1998). Less-efficient but more ubiquitous routes are through ciliates, the top carnivores of the microbial loop, to copepods and other mesozooplankton. In spite of the length of the microbial food chain, it is an important nutritional link in the sea, and there is a net balance of photosynthesis over respiration (Williams, 1998). That microbial food chain is of major significance in large parts of the ocean

where there is little production of the larger, nonbacterial phytoplankton, especially in the “clear blue water” in which Darwin suspected there might be life smaller than protozoa. ☐

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