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## Marine Habitats

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### Glossary

**autotroph** An organism that uses carbon dioxide as its source of carbon for new cell growth. Autotrophs can be either phototrophs or chemotrophs.

**chemotroph** An organisms that derives its energy from reduced inorganic or reduced organic compounds.

**chlorophyll** A ubiquitous pigment that is responsible for light energy absorption in the photosynthetic apparatus of most marine phototrophs.

**euphotic zone** The sunlit portion of the water column where there is a sufficient light flux to sustain net photosynthesis, usually the upper 150–200 m in the clearest ocean water.

**genome** The complement of genes present in a living organism that determines its taxonomic structure, metabolic characteristics, behavior, and ecological function.

**habitat** A place of residence that is defined by a suite of physical, chemical, and biological characteristics.

**mixotrophy** A term used to describe the metabolism of a microorganism that can obtain energy, electrons, or carbon (or all three) from more than one conventional source.

**nutrient** One of several organic or inorganic raw materials that are used by microorganisms to sustain their metabolism, for example, nitrate, phosphate, iron, vitamins.

**phototroph** An organism that derives its energy from sunlight, usually through the process of photosynthesis.

**picoplankton** Small (0.2–2 μm in diameter) phototrophic, chemotrophic, or mixotrophic organisms that live in the water column and drift with the ocean currents.

**remote sensing** The indirect measurement of habitat characteristics, for example, by Earth-orbiting satellites.

**turbulence** A physical process resulting from wind stress, ocean circulation, and related processes that is responsible for the exchange of heat and mass between two or more regions of the ocean, for example, the transport of nutrients from the deep sea to the sunlit surface waters.

**twilight zone** The region of the oceanic realm (also called the mesopelagic zone) immediately below the euphotic zone where sunlight is measurable but insufficient to support net photosynthesis, usually between 200 and 1000 m.

### Abbreviations

**ALOHA** A Long-term Oligotrophic Habitat Assessment

**ATP** adenosine triphosphate

**BATS** Bermuda Atlantic Time-series Study

**CZCS** Coastal Zone Color Scanner

**DCML** Deep Chlorophyll Maximum Layer

**DOM** dissolved organic matter

**DON** dissolved organic nitrogen

**HOT** Hawaii Ocean Time-series

**HTL** higher trophic level

**MODIS** Moderate Resolution Imaging Spectroradiometer

**NPSG** North Pacific Subtropical Gyre

**OSP** Ocean Station Papa

**PAR** Photosynthetically Available Radiation

**SEATS** SouthEast Asia Time-Series

**WOCE** World Ocean Circulation Experiment

## Defining Statement

A habitat is the natural abode of an organism. The marine habitat is composed of a diverse spectrum of environments each supporting the proliferation of a diverse assemblage of microorganisms. When habitats vary, for example as a result of seasonal and longer term climate forcing, the diversity and function of the microbial assemblage will also change. The North Pacific Subtropical Gyre (NPSG), one of Earth's largest habitats, is an excellent example of a marine habitat in motion with respect to microbial structure and function.

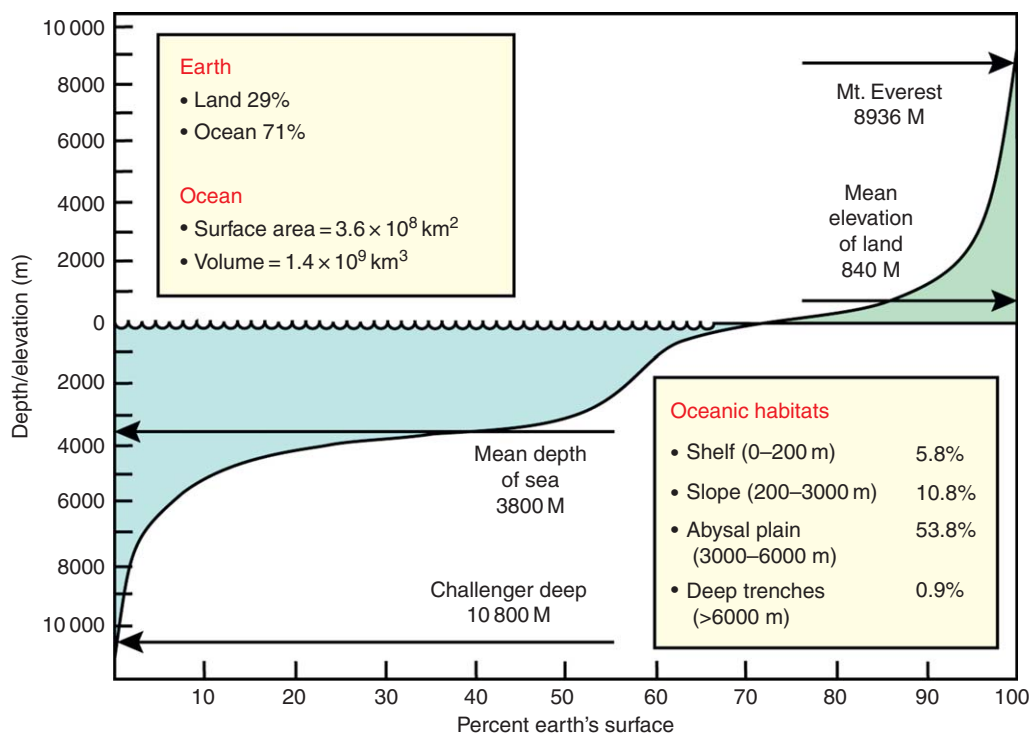
## Introduction

A habitat is often defined as the natural abode or place of residence. For this reason, the global ocean may be considered as one of the largest and oldest habitats on Earth; it covers 71% of the Earth's surface to a mean depth of 3.8 kilometers and comprises >95% of Earth's probable living space (Figure 1). However, despite the appearance of homogeneity, the ocean is actually a complex mosaic of many different macrohabitats that can be identified, studied, and compared; each macrohabitat has a potentially distinct assemblage of microorganisms. Examples are

rocky intertidal, coastal upwelling, deep sea hydrothermal vent, and open ocean habitats.

Some of these habitats are critical to the mass balance of elements in the ocean because they are found at the interface or boundary between terrestrial, or freshwater, and marine systems. For instance, within estuarine habitats, which are located at the freshwater–marine boundary, processes can trap dissolved nutrients and particulate matter, or can export energy in the form of organic matter and nutrients to surrounding coastal habitats. The characteristics of any given estuary will vary depending upon dimensions, hydrology, and geographical location. And, because they represent gradual transition zones, estuaries highlight the difficulty of defining the boundaries of marine habitats. The continental–marine boundary also includes many specialized and important microbial habitats including fjords, salt marshes, mangrove stands, coral reefs, kelp forests, and many man-made or human-impacted (e.g., harbors, sewage outfalls, mariculture farms, gas and oil production facilities) zones.

Another approach to define a marine habitat is through the comprehensive list of physical, chemical, and biological parameters experienced directly by the organism during its lifetime; collectively these parameters determine the success or failure of a particular strain, species, or assemblage of microbes. Given this definition, the size, motility, and



**Figure 1** The world ocean covers 71% of Earth's surface with the deep blue sea (regions seaward of the continental shelf) accounting for more than 60% of the total. With an average depth of 3800 m, the volume of habitable space on planet Earth is dominated by marine habitats. Because microbes dominate the marine environment, they are directly or indirectly linked to most global processes and are largely responsible for the habitability of our planet. Reproduced, with permission, from *Microbial Oceanography* (<http://www.agi.org>).

lifespan of the microbes under consideration define the spatial and temporal scale of their habitat. Hence, it is important to recognize that most microorganisms live in 'microhabitats' that are defined on space scales of micrometers to millimeters and time scales of hours to weeks.

Microhabitats are often the sites of elevated microbial biomass and accelerated metabolism. Once colonized by microorganisms, the environmental conditions within a given microhabitat (e.g., pH, redox level, nutrients, and dissolved gas concentrations) can change as a result of the metabolic activities of the microbial assemblage. Consequently, a description of the macroscopic surrounding habitat (scales of meters to kilometers) may not always be a valid representation of the true habitat of existence. This is the reason why otherwise incompatible microbes, for example, obligate aerobic and anaerobic microorganisms can co-occur in a single environmental sample. Therefore, any given marine habitat – particularly when viewed on macroscale (meter or more) – is likely to be composed of numerous microhabitats that collectively support the growth and proliferation of the microbial assemblage as a whole.

Historically, there has been a concerted effort to define only the physical/chemical properties of a given marine habitat, but more recently the key role of biotic factors in establishing and maintaining microbial community structure and function has been recognized. Many microorganisms in the sea live attached to surfaces including nonliving particulate matter and living organisms. These surfaces help to create and sustain the above-mentioned microhabitats; at the same time they provide local enrichments of organic matter. In addition, bacteria and other microbes can also be found within the digestive tracts of marine macroorganisms, from small crustaceans to large cetaceans; it is likely that every macroorganism in the sea has a unique, species-specific set of microbial partners that are not commonly found elsewhere. And, because many marine macroorganisms (e.g., tuna, squid, and seabirds) have broad geographical distributions and enormous migratory capability, these animal vectors may affect the geographic distribution range of their microbial partners. Additional biotic interactions include virus–host interactions, gene exchange between otherwise unrelated microorganisms, microbe–microbe and microbe–macroorganism symbioses, obligate metabolic partnerships (syntrophy), and coevolution of different groups of microorganisms.

At a microbial level, for many syntrophic relationships to succeed there needs to be a high probability of juxtaposition of cell types to maximize interspecific interactions. This can be achieved in a homogeneous environment where microbes live freely but in close proximity, or through an ordered spatial structure of the microbial assemblage as a whole. In marine sediments and other 'solid' habitats, for example, microbial communities are often established along diffusion gradients with each cell

type growing in the most favorable microhabitat within the gradient in order to maximize success. Growth along these stable gradients, where stability is defined as a function of microbial generation time, can lead to the development of microbial (usually bacterial) mats. Analogous features termed microbial lens or plates can occur in highly stratified 'fluid' habitats, for example, at the oxic–anoxic boundaries of permanently anoxic basins such as the Black Sea or Cariaco Basin. Metabolic activities of microorganisms in these mats and lens can be very high, thereby producing extremely steep vertical gradients of biomass and other metabolic by-products.

Even though we know that microbes are by far the largest contributors to living matter in the sea and have been responsible for the development of the atmosphere under which terrestrial life evolved, much of the research on the role of the habitat in structuring marine microbial communities and their ecosystem function is fairly new, incomplete and lacking any formal theoretical description or predictive capability under changing habitat conditions. And, because seascapes are changing, in part, due to the activities of human populations, a comprehensive understanding of sea microbes and their activities under various global environmental change scenarios is a major and urgent intellectual challenge.

## Nature of Marine Microbial Life

Life on Earth most likely began in the sea; so the marine environment was the original habitat for the growth and proliferation of microorganisms. As the pioneering prokaryotes evolved into more complex life forms, including multicellular macroscopic organisms, and radiated into freshwater habitats and eventually onto land, the imprint of a marine origin remained. Today, virtually all life is intimately dependent upon the availability of water; even desert microbes are aquatic.

Aquatic habitats are built around the unique properties of water. The most important criterion is the fact that water is a polar molecule having positively and negatively charged sides. This characteristic establishes its high dielectric constant and effectiveness as a solvent, setting the stage for the high dissolved ionic (salt) composition of seawater (referred to as salinity). During the HMS *Challenger* expedition of 1872–1876, the 'law of constant proportions' was confirmed, namely that the ratios of the major ions in seawater are relatively constant throughout the world ocean. This relative ionic stability has very important implications for the evolution of marine microorganisms. Furthermore, the unique solvation property of water also facilitates nutrient delivery to and waste material export from the cell, thereby sustaining microbial metabolism.

Other water properties including density and gas solubility, which vary with temperature and salinity, can also

have major implications for the distribution and abundance of microorganisms. The density of pure water at 4 °C is 1.000 g cm<sup>-3</sup>, decreasing slightly to 0.994 g cm<sup>-3</sup> at 35 °C; the average density of seawater is ~1.025 at 25 °C (in marine sciences, the density is often expressed as an anomaly ((density-1.000) × 1000], to amplify the small differences in density between freshwater and seawater; for example, the density anomaly of average seawater would be ((1.025-1.000) × 1000] or 25.0). This means that river and rain water will float on seawater, as will surface waters warmed by the sun, whereas colder and saltier seawater will sink. As a result, the world's ocean is highly stratified with depth; mass exchange and transport occur mainly within layers of constant density (along isopycnals) or via turbulent mixing of waters with different densities (across isopycnals). Diffusional exchange processes that depend on molecular kinetic energy are, by comparison, very slow. This vertical density stratification, a hallmark of the marine environment, tends to insulate inorganic nutrient-rich deep seawaters from the sunlit surface region where the capture of solar energy by biological systems (photosynthesis) occurs. Consequently, density stratification strongly influences the rate of organic matter production and attendant ecosystem services.

In order for marine organisms to live in the water column they need to remain in suspension. The specific gravity of marine microbes varies with their bulk chemical composition (e.g., protein = 1.5 g cm<sup>-3</sup>, nucleic acids = 2.0 g cm<sup>-3</sup>, lipids = 0.9 g cm<sup>-3</sup>) which is, in turn, dependent upon nutrient supply, growth rate, and other biotic factors. If the mean cell density is less than the density of seawater, the cells will tend to rise. Conversely, if the bulk cell density is greater than seawater or if microbes are attached to dense particulate materials, cells will settle. Many marine microorganisms adjust their density by the formation (or collapse) of gas vacuoles, alterations in the ionic composition of the cytoplasm, or by adjusting the above-mentioned composition of the cell, for example, by the synthesis of storage components such as carbohydrates that can serve as ballast. The rate at which cells will rise or settle is also related to their size causing small cells to remain suspended in their environment. Furthermore, most microorganisms, even small bacteria, are motile by means of one or more flagella, but movement through a relatively viscous medium at low Reynold's numbers can be difficult (the Reynold's number is a dimensionless metric that determines whether inertial or viscous forces dominate motion of an object in a fluid). Small bacteria and virus particles are also displaced by means of Brownian motion, a process driven by the random movement of water molecules that can act as a counterforce to gravitational settling. However, even though many marine microorganisms in the water column are motile, their directed movements are small relative to the marine currents in which they reside. Hence, they drift with the

currents and are commonly known as plankton (from the Greek root *Plankto*, which means 'wandering').

In addition to its role in density stratification, solar radiation provides most of the energy required to fuel the biological activity in marine environments. Water has a characteristic solar absorption spectrum that allows electromagnetic radiation between ~350 and 700 nm to penetrate to various depths in the water column depending upon surface solar irradiance, sun angle, and water clarity; the euphotic zone is generally defined as the water column region located above a specific isolume (a constant daily level of irradiance) or above a specific percentage (usually 1 or 0.1%) of the surface irradiance. The water absorption spectrum, with a maximum transmission at 417 nm, creates a sharp gradient, in terms of both the intensity and the quality of light available as a function of depth. For example, while photosynthetic organisms confined to surface waters are exposed to high light intensities within a broad spectrum range within the visible (400–700 nm) and extending into the near-ultraviolet region (350–400 nm), deeper marine habitats experience lower light intensities due to the exponential decrease of light with depth and a shift toward a dominance of blue light. Hence, while organisms in surface waters have had to adapt to protect themselves against excess light and ultraviolet radiation by producing photoprotective pigments, organisms living near the base of the euphotic zone require strategies that increase their capabilities of solar energy capture in the blue region of the spectrum; this is achieved by increasing the number of photosynthetic units per cell and by modifying the spectral absorption characteristics through changes in the photosynthetic pigments associated with them. As a consequence, the light gradient can generate and sustain a highly structured vertical pattern of light-harvesting microorganisms in the marine environment; some microbes are adapted to high and others to lower light fluxes. In addition, the surface light intensity and its propagation through the water column define the region where the photosynthetic rates of the microbial assemblage can exceed its respiration, driving the balance between the uptake (photosynthesis) and remineralization (respiration) of nutrients with depth. It is this balance in microbial activity that ultimately drives the biological sequestration and transport of elements, such as carbon, in the ocean and defines the large-scale distribution and availability of nutrients in the marine environment.

### Structure and Classification of Marine Macrohabitats

There are numerous criteria that can be used to classify marine habitats. The most widely accepted scheme divides the ocean into two broad categories: pelagic and benthic,

**Table 1** Classification of marine habitats according to Hedgpeth (1957)

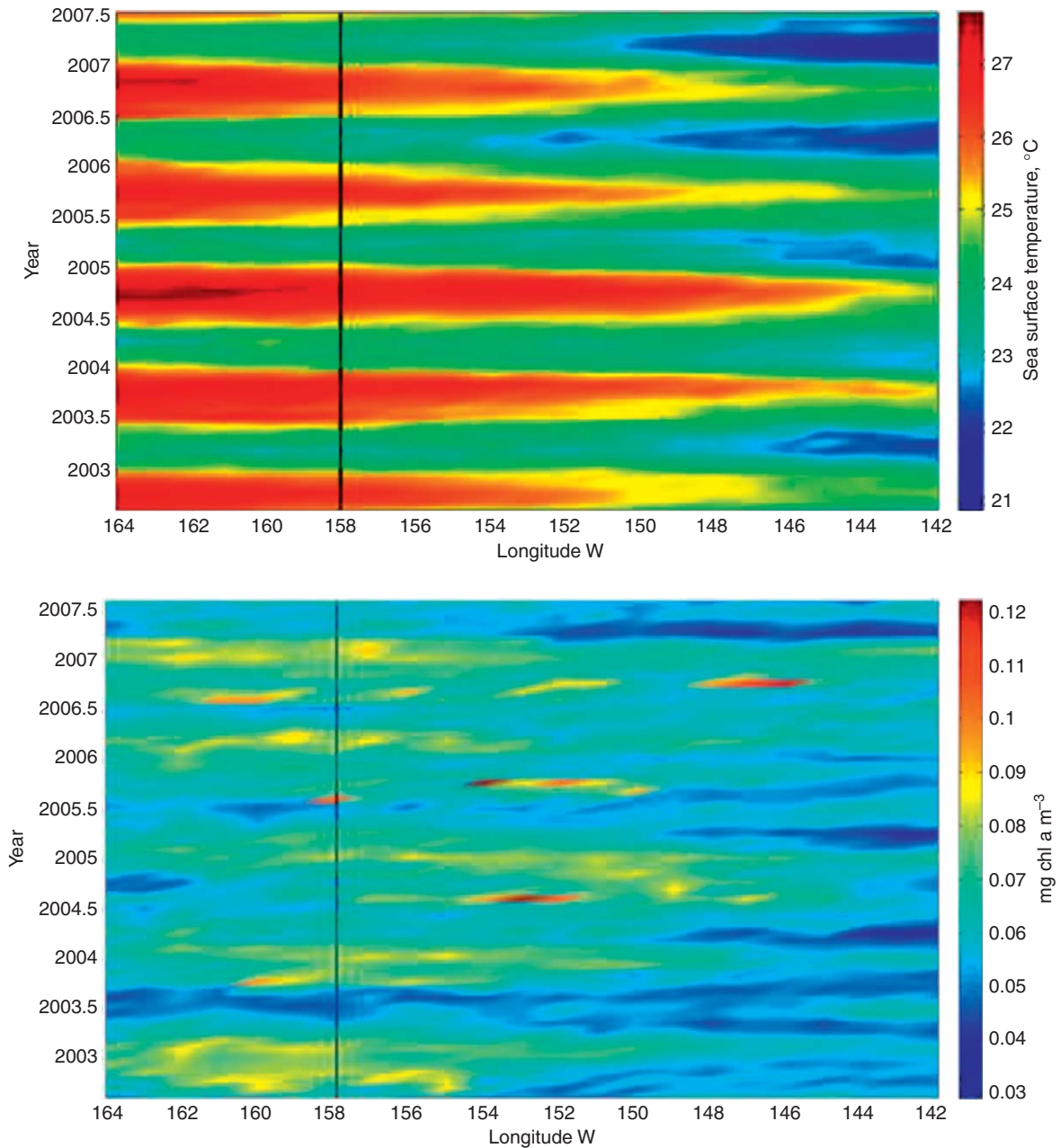
Region	Boundaries/comments
<b>Pelagic Realm (water column)</b>	
Neritic	Waters over the continental shelves (~200 m)
Oceanic	Waters seaward of the continental shelves
- epipelagic	0–200 m; sunlit regions
- mesopelagic	200–1500 m
- bathypelagic	1500–4000 m
- abyssopelagic	>4000 m
<b>Benthic Realm (seabed)</b>	
Supralittoral	Above high-tide mark
Littoral	Between the tides
Sublittoral	Between low tide and edge of continental shelves (~200 m)
Bathyal	Seaward of continental shelves to ~4000 m
Abyssal	4000–6000 m
Hadal	>6000 m, including trenches

depending upon whether the habitat of interest is the overlying water column (fluid) or the seabed (solid), respectively (Figure 1; Table 1). Within each of these main categories, a number of additional subdivisions can be made depending, for example, on increasing water depth from the high tide mark. For the pelagic habitat, major subdivisions include neritic for waters overlying the continental shelves ( $\leq 200$  m deep) and oceanic, for the vast open sea. The oceanic realm can also be further subdivided (Table 1). Benthic habitats include littoral (intertidal), sublittoral (from the low tide boundary to edge of continental shelf), bathyal, abyssal, and hadal. Other classification schemes use the topographic boundaries: continental shelf, continental slope, abyssal plain, and deep sea trenches (see Figure 1). Although these and other terms are routinely used, the depth ranges are not always identical, so they should be considered as guidelines rather than rules.

Along the seawater depth gradient, whether in benthic or pelagic habitats, some physical and chemical characteristics systematically change (e.g., decreasing temperature and increasing pressure). In this regard, it is important to emphasize that the most common marine habitat is cold ( $< 12^\circ\text{C}$ ) and exposed to high hydrostatic pressure ( $> 50$  bars). Consequently, many marine microbes are cold- and pressure-adapted, even obligately so; indeed, some abyssopelagic bacteria require high pressure ( $> 400$  bars) to grow. Other classification schemes based on the availability of sunlight (euphotic (light present) or aphotic (light absent)) or the relative rates of organic matter production (eutrophic (high), mesotrophic (medium), or oligotrophic (low)) have also been used.

Sharp horizontal gradients can also be observed in the surface of the ocean. For example, since the 1960s, oceanographers have used satellite-based remote sensing approaches to map various features of the global ocean, including sea surface temperature, winds, altimetry, and the distributions of photosynthetic microbes as inferred from observations of spectral radiance. The first satellite-based ocean color measurements were obtained using the Coastal Zone Color Scanner (CZCS) aboard the Nimbus-7 satellite that was launched in October 1978; it provided useful data for nearly a decade. The CZCS sensor was eventually replaced with the Sea-viewing Wide Field-of-view Sensor (SeaWiFS), launched in September 1997, and still operational, followed by Moderate Resolution Imaging Spectroradiometer (MODIS) aboard the Terra and Aqua satellites (1999 and 2002 to present, respectively). And, although these instruments cannot provide information regarding spatial variability below 1 km resolution, they have provided unprecedented observations on the temporal variability or surface ocean macrohabitats (depth-integrated to one optical depth,  $\sim 25$  m in clear open ocean waters), as well as the mesoscale (10–100 s of km) and large-scale distributions of chlorophyll (chl). Daily synoptic global images can be pieced together to track the dynamics (days to decades) of photosynthetic microbial assemblages in the global ocean and their correlations with other environmental variables in ways that are not possible by any other means (Figure 2). Furthermore, systematic analyses of these ocean color datasets can be used to define spatial habitat structure in oceanic ecosystems, and the partitioning of the global ocean into a suite of ecological provinces or functional habitat units, leading to the novel subdiscipline of marine ecological geography. Unfortunately, there are no satellite-based sensors that can track non-chl-containing marine microbes, although several novel remote detection systems are under development for *in situ* application based on molecular/genetic probes and imaging-in-flow cytometry.

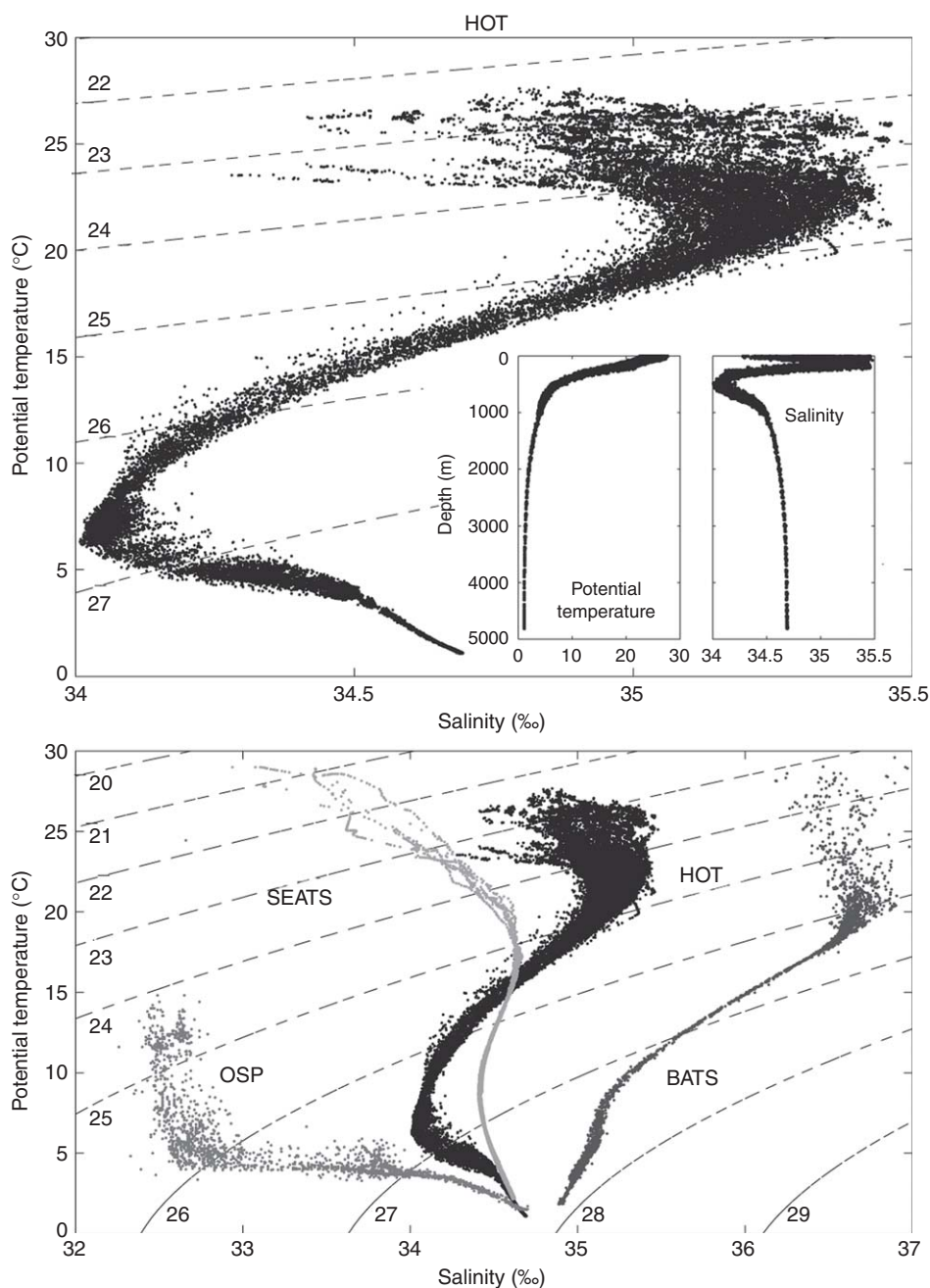
There are distinct water types throughout the ocean that can be easily identified by measuring their temperature and salinity characteristics, which together determine their densities (T-S diagram; Figure 3). Using T-S diagrams as a fingerprinting tool, water types can be traced throughout the world ocean to specific regions of formation. A water mass results from the mixing of two or more water types, and is represented by a line between distinct water types on the T-S diagram (Figure 3). Water masses can also be tracked for great distances throughout the world ocean, and their microbial assemblages can also be sampled and characterized. The global circulation rate, as deduced by nonconservative chemical properties and radioisotopic tracers, has a time scale of hundreds to thousands of years. Consequently, 'young' and 'old' water masses can be identified based on the time that the water was last in contact with the atmosphere.



**Figure 2** Satellite-derived temporal and longitudinal variability in sea surface temperature (Top) and chlorophyll (Bottom) for the region surrounding Station ALOHA (22.75°N, 158°W). The data, available from the NASA Ocean Color Time-Series Online Visualization and Analysis website (<http://reason.gsfc.nasa.gov/>), have been obtained through NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on board Aqua between July 2002 and June 2007 and correspond to the latitudinal average between 22.5°N and 23.5°N for the longitude band 142–164°W. The black line marks longitude 158°W where Station ALOHA is located.

Due to unique seafloor topography and interactions with the atmosphere, certain regions 'short-circuit' the mean circulation by serving as conduits for a more rapid ventilation of the deep ocean (bringing it into contact with the atmosphere) and the concomitant delivery of nutrient-rich deep water to the surface of the sea. These so-called upwelling regions occupy only ~1% of the

surface ocean, but they are important areas of solar energy capture through enhanced photosynthesis and the selection of relatively large algae and short food chains; thereby they support some of the great fisheries of the world (Figure 4). In contrast, the more common condition (90% of the global ocean) is the oligotrophic habitat (low nutrient and low rates of organic

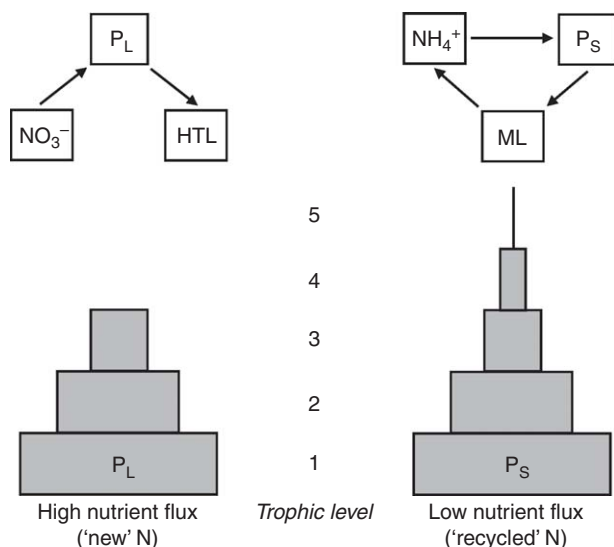


**Figure 3** Potential temperature versus salinity (T-S) plots are used to identify, trace, and compare distinct water types and water masses in the marine environment. (Top) T-S diagram for the Hawaii Ocean Time-series (HOT) Station ALOHA for the period 1988–2006. The inset shows the depth profiles of potential temperature and salinity. The ALOHA T-S fingerprint shows the presence of numerous water masses at specific depths. The contours show lines of constant density, or isopycnal surfaces, in density anomaly notation ((density in  $\text{g cm}^{-3}$ )–1.000)×1000). In addition to temperature and salinity (density) variations, these distinctive water masses also have distinctive chemical properties and may contain unique assemblages of microorganisms. The large variability of T and S at the top of the graph is a result of seasonal and interannual changes in near-surface water properties. (Bottom) Comparison of T-S fingerprints for a variety of oceanic time-series stations including: Ocean Station Papa (OSP; 50°N, 145°W), SouthEast Asia Time-Series (SEATS; 18°N, 116°E), Hawaii Ocean Time-series (HOT; 22.75°N, 158°W), and Bermuda Atlantic Time-series Study (BATS; 32°N, 64°W). The three North Pacific stations (OSP, SEATS, HOT) have a common deep water mass.

matter production) that selects for very small primary producers, long and complex microbial-based food webs, and relatively inefficient transfer of carbon and energy to higher trophic levels like fish. These

fundamental differences in physics result in marine habitats with diverse structures and dynamics that host dramatically different microbial assemblages, as discussed later in this article.





**Figure 4** Importance of nutrient flux on the size distribution and efficiency of biomass and energy flow in marine habitats. The schematic on the left depicts a habitat where ‘new’ nutrient (as  $\text{NO}_3^-$ ) flux is high (e.g., an upwelling region). This leads to a selection for large phytoplankton cells ( $P_L$ ) that are efficiently consumed by higher trophic levels (HTLs) including large zooplankton and fish. This results in a short and efficient food chain. In contrast to the upwelling regions, most open ocean habitats have low new nutrient ( $\text{NO}_3^-$ ) fluxes and survive by local remineralization of required nutrients (‘recycled’). These conditions select for small phytoplankton cells ( $P_S$ ) that serve as the food source for long and complex microbial-based food webs (also called microbial loops; ML) that recycle mass and dissipate most of the solar energy that was initially captured. The great marine fisheries of the world are generally found in association with upwelling regions.

### Marine Microbial Inhabitants and Their Growth Requirements

The marine environment supports the growth of a diverse assemblage of microbes from all three domains of life: *Bacteria*, *Archaea*, and *Eucarya*. The term ‘microorganism’ is a catchall term to describe unicellular and multicellular organisms that are smaller than  $\sim 100\text{--}150\ \mu\text{m}$ . This grouping includes organisms with broadly distinct evolutionary histories, physiological capabilities, and ecological niches. The only common, shared features are their size and a high surface-to-biovolume ratio. A consequence of being small is a high rate of metabolism and shorter generation times than most larger organisms.

Microorganisms, particularly bacteria and archaea, are found throughout the world ocean including marine sedimentary and subseabed habitats. There is probably no marine habitat that is devoid of microorganisms, with the possible exception of high-temperature ( $>100^\circ\text{C}$ ) zones. In addition to a physically favorable environment, the metabolism and proliferation of microorganisms also require a renewable supply of energy, electrons for energy generation,

**Table 2** Variations in microbial metabolism based on sources of energy, electrons, and carbon according to Karl (2007)

Source of energy <sup>a</sup>	Source of electrons	Source of carbon
Sunlight photo-	Inorganic	$\text{CO}_2$
	-litho-	-autotroph
	Organic	Organic
Chemical chemo-	-organo-	-heterotroph
	Inorganic	$\text{CO}_2$
	-litho-	-autotroph
Radioactive decay radio-	Organic	Organic
	-organo-	-heterotroph
	Inorganic	$\text{CO}_2$
	-litho-	-autotroph
	Organic	Organic
	-organo-	-heterotroph

<sup>a</sup>A ‘mixotroph’ is an organism that uses more than one source of energy, electrons, or carbon.

carbon (and related bioelements including nitrogen, phosphorus, sulfur), and occasionally organic growth factors such as vitamins. Depending upon how these requirements are met, all living organisms can be classified into one of several metabolic categories (Table 2). For example, photolithoautotrophic microbes use light as an energy source, water as an electron source, and inorganic carbon, mineral nutrients, and trace metals to produce organic matter. At the other end of the metabolic spectrum, chemoorganoheterotrophic microbes use preformed organic matter for energy generation and as a source of electrons and carbon for cell growth. In a laboratory setting, only obligate photolithoautotrophs are self-sufficient; all other autotrophs and all heterotrophs rely upon the metabolic activities of other microorganisms. However in nature, even obligate photolithoautotrophs must tie their growth and survival to other, mostly deep-sea, microbes that are vital in sustaining nutrient availability over evolutionary time scales. Most marine microorganisms probably use a variety of metabolic strategies, perhaps simultaneously, to survive in nature. Because needed nutrients in the ocean’s surface are often found in dissolved organic molecules, it seems highly improbable that sunlit marine habitats would select for obligate photolithoautotrophy as opposed to, for instance, mixotrophic growth.

Across the full metabolic spectrum of possible modes of growth, some microbes are more self-sufficient than others. For example, while most microbes require a supply of chemically ‘fixed’ nitrogen, either in reduced (ammonia or dissolved organic nitrogen (DON)) or in oxidized (nitrate or nitrite) form to survive, a special group of  $\text{N}_2$ -fixing microbes (diazotrophs) can use the nearly unlimited supply of dissolved  $\text{N}_2$  as their sole source of cell N. Additionally, some microbes can manufacture all their required building blocks (e.g., amino acids and nucleic acid bases) and growth cofactors (e.g., vitamins) from simple inorganic precursors, whereas others

require that they be supplied from the environment; 'auxotrophic' microorganisms are, therefore, ultimately dependent upon the metabolic and biosynthetic activities of other microbes. These 'incomplete' microbes, probably the bulk of the total microbial assemblage in seawater, cannot grow unless the obligate growth factors are present in and resupplied to the local habitat. In this regard, most marine habitats provide the laboratory equivalent of a complex or complete medium containing low-molecular-weight compounds (e.g., amino acids, simple sugars, nucleic acid bases, and vitamins), in addition to the mineral nutrients and trace metals. The active salvage and utilization of these biosynthetic precursors, in lieu of *de novo* synthesis, conserves energy, increases growth efficiency, and enhances survival. Over evolutionary time, some unused biosynthetic pathways in particular organisms appear to have been lost from the genome, perhaps, as a competitive strategy for survival in a mostly energy-limited environment. This process has been termed genome streamlining.

Finally, growth and reproduction are often viewed as the most successful stages of existence for any microorganism. However, in many of the low nutrient concentration and low energy flux habitats that dominate the global seascape, the ability to survive for extended periods under conditions of starvation may also be of great selective advantage and ultimately may affect the stability and resilience of microbial ecosystems. The starvation-survival response in marine bacteria leads to fragmentation (i.e., cell division in the absence of net growth) and, ultimately, to the formation of multiple dwarf or miniaturized cells. Other physiological changes, including reduction in endogenous metabolism, decreases in intracellular adenosine triphosphate (ATP) concentrations, and enhanced rates of adhesion are also common consequences. These starved cells can respond rapidly to the addition of organic nutrients. This 'feast and famine' cycle has important implications for how we design *in situ* metabolic detection systems and model microbial growth in marine habitats.

### Distribution, Abundance, and Biogeography of Marine Microbes

The distribution and abundance of microbes is highly variable, but somewhat predictable, across globally distributed marine habitats. For example, phototrophic microbes are restricted to sunlit regions (0–200 m in the open sea) whereas chemotrophic microbes are found throughout the oceanic realm. However, because the abundance and productivity of marine microbes depend on the availability of nutrients and energy, there is often a decreasing gradient in total microbial biomass from the continents to the open ocean, and a decreasing gradient in total microbial biomass from the sunlit surface waters to the abyss. For the pelagic

zone, total microbial biomass in near-surface (0–100 m) waters ranges from 30 to 100 mg carbon  $\text{m}^{-3}$  in neritic waters to 6–20 mg carbon  $\text{m}^{-3}$  in oceanic waters. For open ocean habitats, this biomass decreases by approximately three orders of magnitude from euphotic zone to abyssal habitats, with values  $<0.02$  mg carbon  $\text{m}^{-3}$  in the deepest ocean trenches. When scaling these concentrations to the volume of the ocean, the total oceanic microbial biomass, excluding sediments, has been estimated to be  $0.6\text{--}1.9 \times 10^{15}$  g carbon with approximately half its stock residing below 100 m.

Temperature is an important habitat variable, and may be responsible for structuring microbial assemblages and setting limits on various metabolic processes. However, temperature *per se* does not limit the existence of marine microbes so long as liquid water exists. Accordingly, there are some marine habitats that select for thermophilic microbes ('warm temperature-loving'; e.g., deep-sea hydrothermal vents) and others for psychrophilic microbes ('cold temperature-loving'; e.g., polar latitudes and abyssal regions). Spatial gradients in temperature across open ocean habitats as well as seasonal changes in temperature can also affect the diversity of microbial assemblages in most marine habitats. Finally, for any given microbial species, there is a positive correlation between rates of metabolism and temperature over its permissive range. Generally, for a  $10^\circ\text{C}$  change in temperature there is a two- to threefold increase in metabolic activity, for example, respiration. Photochemical reactions, including photosynthesis, have much smaller temperature coefficients, and it has been hypothesized that low temperature suppression of chemoorganoheterotrophic bacterial activity, relative to photosynthesis, might significantly restrict energy flow through microbial food webs, increasing the efficiency of the transfer of carbon and energy to higher trophic levels via metazoan grazing. This is just one way in which temperature may structure and control microbial processes in the sea.

In the near-surface waters, microbes capture solar energy, which is locally transferred and dissipated as heat, or exported to other surrounding marine habitats in the form of reduced organic or inorganic substrates, including biomass. Apart from very restricted shallow coastal regions where light can penetrate all the way to the seabed for use by benthic micro- and macroalgae, essentially all marine photosynthesis is planktonic (free floating) and microbial. The dynamic range in total marine photosynthesis, from the most productive to the least productive regions of the global ocean, is probably less than two orders of magnitude for a given latitude, and the biomass of chemoorganoheterotrophic bacteria may be even less. There are much steeper gradients in photosynthesis and bacterial/archaeal biomass in the vertical (depth) than with horizontal (spatial) dimensions. Furthermore, most marine respiration is also driven by microbes, both phototrophs and chemotrophs. For this reason, the mean turnover time of oceanic carbon within

biological systems in surface waters is weeks, compared to decades for most terrestrial ecosystems.

Size spectral models and analyses, which relate the relative abundance of organisms as a function of size, have been used to examine the distribution of biomass among various size classes. The emergent patterns from these analyses, particularly between and among different marine habitats, are relevant to issues regarding the environmental controls on microbial community structure and function as well as to the trophic efficiency of marine food webs. In some oceanic habitats, solar energy is captured and completely utilized within microbial-based food webs; in other regions a significant proportion of the energy captured via photosynthesis is passed to large organisms, including fish and humans. An important consideration appears to be the size of the primary producer populations, and this determines the number of trophic transfers that are sustainable in light of the typically inefficient (<10%) transfer of carbon and energy between trophic levels (Figure 4). If, for example, the primary producers are relatively large (>10–20 µm diameter;  $P_L$  in Figure 4, left), such as unicellular algae including diatoms, rather than tiny picoplankton (<2 µm;  $P_S$  in Figure 4, right), then the grazer/consumer based food chain is shorter, leading to a more efficient transfer of carbon and energy (Figure 4). However, the length of the food chain is not always defined by the difference in size between the primary producer and the top consumer; in some cases, large organisms such as baleen whales have adapted a feeding strategy that relies mostly on very small, planktonic organisms. Nevertheless, the size and structure of marine food webs is determined, in large part, by physical processes such as turbulence, which, in turn, affects the flux of nutrients into the euphotic zone and, therefore, shapes the structure and function of marine ecosystems.

In most sunlit marine habitats there is generally a significant correlation between chl concentrations and the number of bacterial cells, and between net primary production and bacterial production across a broad range of ecosystems. These empirical relationships suggest that phototrophs and chemotrophs grow in response to common factors (e.g., nutrients, temperature), or that phototrophs produce substrates for the growth of chemotrophs, or vice versa.

In addition to living organisms, virus particles – particularly those capable of infecting specific groups of microorganisms – can exert influence on microbial-based processes. For example, through microbial infection and subsequent lysis, viral activity may directly influence the composition of the microbial assemblage. Furthermore, through the release of dissolved organic matter (DOM) into the marine environment during virus-induced cell lysis, an indirect effect on metabolic activity of the chemotrophic assemblage can occur. Viruses can also

facilitate genetic exchange between different microbial strains contributing to the metabolic plasticity of certain microorganisms and the redundancy of some metabolic processes in a given environment. It has been reported that virus particle abundances closely track the abundance of bacteria plus archaea, at least in the water column, with virus-to-prokaryote ratios ranging from 5 to 25, and commonly close to 10. This relationship appears to hold even into the deep sea, suggesting a close ecological linkage throughout the entire marine habitat.

From an ecological perspective, understanding and modeling how microbial assemblages emerge as a result of interaction of physics and biology is a primary goal in microbial oceanography. In this context, the study of the distribution of biodiversity over space and time, also known as biogeography, seeks fundamental information on the controls of speciation, extinction, dispersal and species interactions such as competition. The field of microbial biogeography is just beginning to develop a conceptual framework and analytical tools to examine distribution patterns and to quantify diversity at the ecologically relevant taxonomic scale. For example, recent studies of the marine phototroph *Prochlorococcus* have documented significant intraspecific genomic variability that confers distinct niche specificity including nutrient and light resource partitioning. What appears at one level to be a cosmopolitan species is actually a group of closely related ecotypes (populations within a species that are adapted to a particular set of habitat conditions); the high- and low-light ecotypes have >97% similarity in their 16S ribosomal RNA gene sequences and share a core of 1350 genes, but vary by more than 30% in their total gene content (and genome size; the high- and low-light adapted ecotypes have genome sizes of 1 657 990 bp and 2 410 873 bp, respectively). An assemblage of related *Vibrio splendidus* (>99% 16S RNA identity) sampled from a temperate coastal marine habitat had at least 1000 distinct coexisting genotypes, and bacterial samples collected from the aphotic zone of the North Atlantic Ocean revealed an extremely diverse 'rare biosphere' consisting of thousands of low-abundance populations. The ecological implications of these independent reports of taxonomic diversity are profound; new ecological theory may even be required to build a conceptual framework for our knowledge of marine habitats and their microbial inhabitants.

### Sunlight, Nutrients, Turbulence, and the Biological Pump

Of all the environmental variables that collectively define the marine habitat, we single out three – namely, sunlight, nutrients, and turbulence – as perhaps the most critical for the survival of sea microbes. Together, these properties

control the magnitude and efficiency of the 'biological pump', a complex series of trophic processes that result in a spatial separation between energy (sunlight) and mass (essential nutrients) throughout the marine environment. In the sunlit regions of most (but not all) marine habitats, nutrients are efficiently assimilated into organic matter, a portion of which is displaced downward in the water column, mostly through gravitational settling. As particles sink through the stratified water column, a portion of the organic matter is oxidized and the essential nutrients are recycled back into the surrounding water masses. Depending upon the depth of remineralization and replenishment to the surface waters by physical processes, these essential nutrients can be sequestered for relatively long periods (>100 yrs). The vertical nutrient profile, for example of nitrate, shows a relative depletion near the surface and enrichment at depth as a result of the biological pump (Figures 5(a) and 5(b)); regional variations in the depth profiles reflect the combination of changes in the strength and efficiency of the biological pump and the patterns of global ocean circulation (Figures 5(a) and 6). The highest nutrient concentrations in deep water can be found in the abyss of the North Pacific, the oldest water mass on Earth. The regeneration of inorganic nutrients requires the oxidation of reduced organic matter, so the concentrations of dissolved oxygen decrease with depth and with age of the water mass as a result of the cumulative effect of microbial metabolism (Figures 5(b) and 6).

Turbulence in marine habitats derives from a variety of processes including wind stress on the ocean's surface, ocean circulation, breaking internal waves, and other large-scale motions that can create instabilities, including eddies, in the mean density structure. Turbulence, or eddy diffusion, differs fundamentally from molecular diffusion in that all properties (e.g., heat, salt, nutrients, and dissolved gases) have the same eddy diffusion coefficient; a typical value for horizontal eddy diffusivity in the ocean is  $\sim 500 \text{ m}^2 \text{ s}^{-1}$ , a value that is  $10^9$  times greater than molecular diffusion. Vertical eddy diffusivity is much lower ( $\sim 0.6\text{--}1 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$ ) suggesting that the upward flux of nutrients into the euphotic zone is a slower process than movement horizontally in the open ocean. Most near-surface dwelling microbes, particularly phototrophs that are also dependent upon solar energy and are effectively 'trapped' in the euphotic zone habitat, depend on turbulence to deliver deep water nutrients to the sunlit habitat.

In addition to the eddy diffusion of nutrients from the mesopelagic zone, wind stress at the surface and other forces can mix the surface ocean from above. If the near-surface density stratification is weak or if the mixing forces are strong, or both, then a large portion of the euphotic zone can be homogenized; in selected latitude regions the surface mixing layer can extend to 500 m or more, well below the maximum depth of the euphotic

zone. These well-mixed environments usually have sufficient nutrients but insufficient light to sustain photosynthesis because the phototrophs are also mixed to great depths, as in some polar habitats during winter months. Following these seasonal deep-mixing events, the ocean begins to stratify due to the absorption of solar radiation in excess of evaporative heat loss. As the wind forcing from winter storms subsides and the intensity of solar radiation increases, a density gradient develops in the upper water column. Phototrophic microorganisms in the euphotic zone gain a favorable niche with respect to both light energy and nutrient concentrations. Depending upon the presence or absence of grazers, this condition results in an increase in phototrophic microbial biomass, a condition referred to as the spring bloom. A comprehensive formulation of the 'vernal blooming of phytoplankton' presented by H. Sverdrup remains a valid representation of this important marine microbial phenomenon.

However, in many portions of the world ocean, particularly in tropical ocean gyres, local forcing due to wind stress is too weak to break down the density stratification, so the nutrient delivery from below the euphotic zone through mixing is not possible. In these oligotrophic regions, the habitat is chronically nutrient-stressed and oftentimes nutrient-limited. Although surface mixed layers can be observed, they rarely penetrate deeper than 100 m. Even within the so-called mixed layer, gradients in chl, nutrients, dissolved gases, and microorganisms can be detected, suggesting that these regions are not always actively mixing. This subtle distinction between a mixing layer, where there is an active vertical transport of physical, chemical, and biological properties, and a mixed layer, which is defined operationally as a layer with weak or no density stratification, has important implications for microbial growth and survival, particularly for phototrophic microorganisms. Consequently, without additional information on mixing dynamics (e.g., a profile of turbulent kinetic energy), the commonly used term mixed layer can be misleading with regard to habitat conditions for microbial growth. The time required to change from a mixing layer to a mixed layer to a density-stratified surface habitat and back again will depend on the habitat of interest.

One approach for distinguishing between a mixing layer and a mixed layer is to measure the near-surface concentrations and temporal dynamics of a short-lived photochemically produced tracer, for example, hydrogen peroxide ( $\text{H}_2\text{O}_2$ ). The concentration versus depth profile of  $\text{H}_2\text{O}_2$  in a mixing layer with a short mixing time scale ( $\leq 1$  h) would be constant because the concentration of photochemically active DOM and average solar energy flux would also be relatively constant. On the other hand, the  $\text{H}_2\text{O}_2$  concentration profile in a nonmixing (or slowly mixing, turnover >1 day) 'mixed layer' would

approximate the shape to the flux of solar energy decreasing exponentially with depth nearly identical to a density-stratified habitat, assuming that the concentration of photosensitive DOM is in excess. It is also possible to use other photochemical reactions to obtain information on vertical mixing rates.

### Time Variability of Marine Habitats and Climate Change

Marine habitats vary in both time and space over more than nine orders of magnitude of scale in each dimension. Compared with terrestrial habitats, most marine ecosystems are out of 'direct sight', and, therefore, sparsely observed and grossly undersampled. The discovery and subsequent documentation of the oases of life surrounding hydrothermal vents in the deep sea in 1977 revealed how little we knew about benthic life at that time. Furthermore, because marine life is predominantly microscopic in nature, the temporal and spatial scales affecting microbial processes may be far removed from the scales that our senses are able to perceive. And, due to

this physical and sensory remoteness of marine microbial habitats, even today unexpected discoveries about the ocean frontier continue to be made, many of these involving marine microbes.

We have selected the North Pacific Subtropical Gyre (NPSG) for a more detailed presentation of relationships between and among habitat structure, microbial community function and climate. Our choice of the NPSG as an exemplar habitat is based on the existence of the Hawaii Ocean Time-series (HOT) study, a research program that seeks a fundamental understanding of the NPSG habitat. The emergent comprehensive physical, chemical, and biological data sets derived from the HOT benchmark Station ALOHA (A Long-term Oligotrophic Habitat Assessment) is one of the few spanning temporal scales that range from a few hours to almost two decades. More generally, we submit that the sampling and observational components of the HOT program at the deep water Station ALOHA are applicable to other locations that may be representative of key marine habitats.

The NPSG is one of the largest and oldest habitats on our planet; its present boundaries have persisted since the

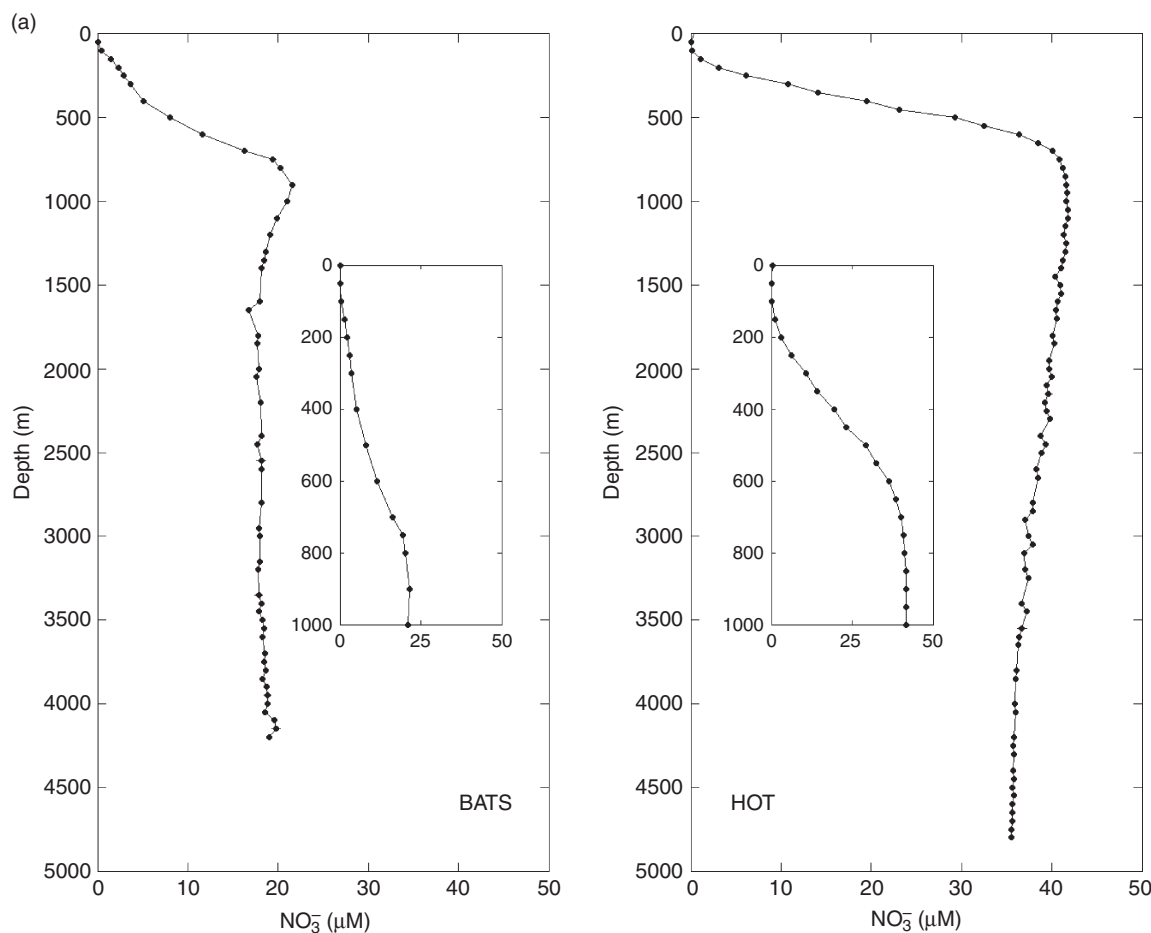
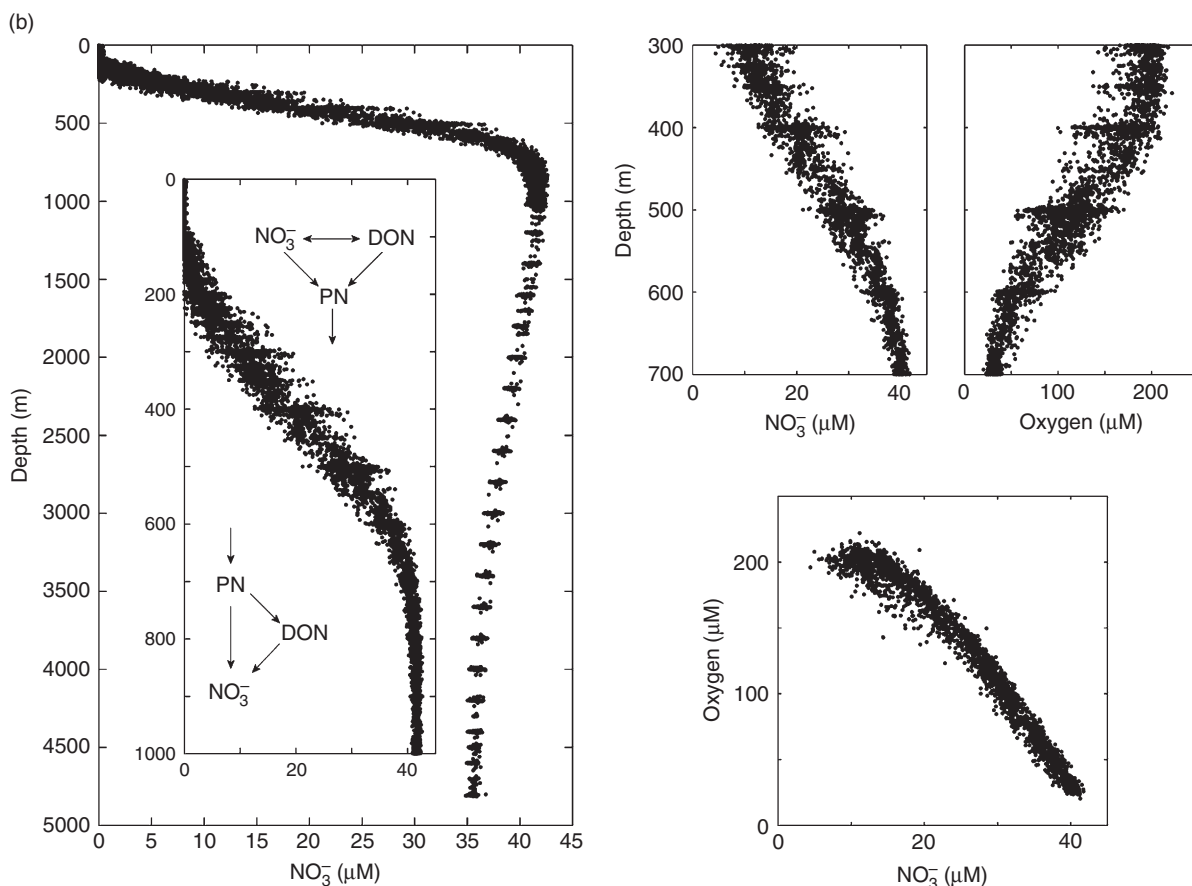


Figure 5 (Continued)



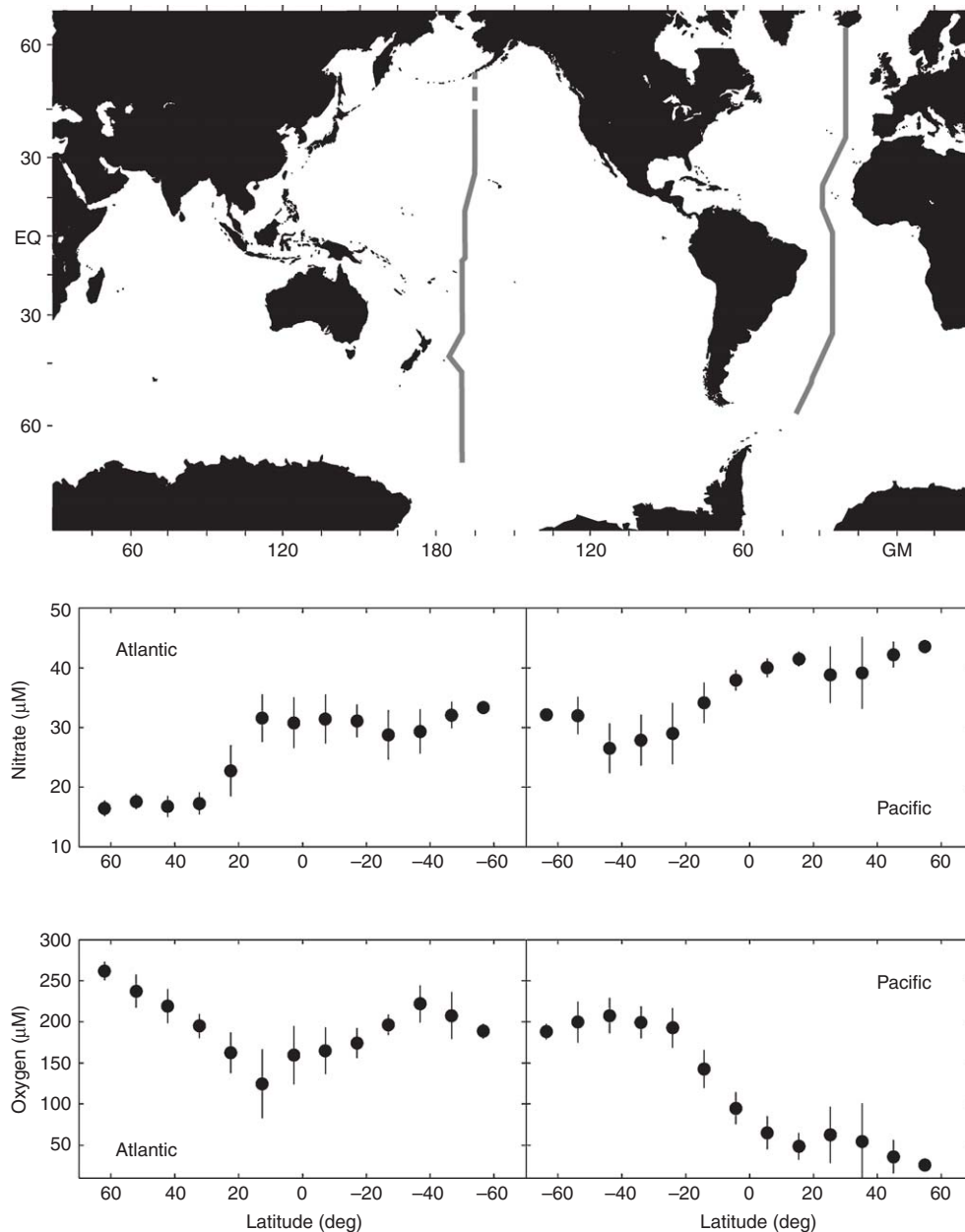
**Figure 5** (a) Nitrate ( $\text{NO}_3^-$ ) versus depth profiles for the North Atlantic (Bermuda Atlantic Time-series Study; BATS) and the North Pacific (Hawaii Ocean Time-series; HOT) showing significant interocean differences including a steeper nitracline (i.e., a larger change in  $\text{NO}_3^-$  concentration per meter in the upper mesopelagic zone region) and higher deep water (>4000 m)  $\text{NO}_3^-$  concentrations for HOT. These differences in  $\text{NO}_3^-$  inventories and gradients, part of a systematic global pattern (see **Figure 6**), have significant implications for  $\text{NO}_3^-$  fluxes into the euphotic zone. Data available at the HOT and BATS program websites (<http://hahana.soest.hawaii.edu>; <http://www.bios.edu/>). (b) Relationships between the vertical distributions of nitrate ( $\text{NO}_3^-$ ) and dissolved oxygen ( $\text{O}_2$ ) at Station ALOHA in the North Pacific Subtropical Gyre (NPSG). (Left) Graph of  $\text{NO}_3^-$  ( $\mu\text{mol l}^{-1}$ ) versus depth (m) showing the characteristic ‘nutrient-like’ distribution of  $\text{NO}_3^-$  with regions of net  $\text{NO}_3^-$  uptake and DON cycling and particulate nitrogen (PN) export near the surface, and net  $\text{NO}_3^-$  remineralization at greater depths. The insert shows these main N-cycle processes, which are most intense in the upper 1000 m of the water column. (Right, top)  $\text{NO}_3^-$  and  $\text{O}_2$  concentration versus depth profiles of the 300–700 m region of the water column at Station ALOHA showing the effects of net remineralization of organic matter. (Right, bottom) A model 2 linear regression analysis of  $\text{NO}_3^-$  versus  $\text{O}_2$  suggests an average consumption of  $80 \mu\text{mol l}^{-1} \text{O}_2$  for each  $1 \mu\text{mol}$  of  $\text{NO}_3^-$  that is regenerated from particulate and DOM. Data available at the HOT program website (<http://hahana.soest.hawaii.edu>).

Pliocene nearly  $10^7$  years before present. The vertical water column at Station ALOHA can be partitioned into three major microbial habitats: euphotic zone, mesopelagic (twilight) zone, and aphotic zone (**Table 3** and **Figure 7**). The main determinant in this classification scheme is the presence or absence of light. The euphotic zone is the region where most of the solar energy captured by phototrophic marine microbes is sufficient to support photosynthetic activity. In the twilight zone (200–1500 m), light is present at very low photon fluxes, below which photosynthesis can occur, but at sufficiently high levels to affect the distributions of mesozooplankton and nekton and, perhaps, microbes as well. At depths greater than  $\sim 1500$  m, light levels are less than  $10^3$  quanta

$\text{cm}^{-2} \text{s}^{-1}$ ; the aphotic zone is, for all intents and purposes, dark.

Each of these major habitats is characterized by specific physical and chemical gradients, with distinct temporal scales of variability, providing unique challenges to the microorganisms that live there, and resulting in a vertical segregation of taxonomic structure and the ecological function of the resident microbial assemblages. A recent report of microbial community genomics at Station ALOHA, from the ocean’s surface to the abyss, has revealed significant changes in metabolic potential, attachment and motility, gene mobility, and host–viral interactions.

The NPSG is characterized by warm ( $>24^\circ\text{C}$ ) surface waters with relatively high light and relatively low



**Figure 6** Map showing the locations of the World Ocean Circulation Experiment (WOCE) program transects A-16 (Atlantic) and P-15 (Pacific). Data from these cruises were obtained from <http://woce.nodc.noaa.gov> and averaged over the depth range of 500–1500 m, then combined into 10° latitude bins and plotted as mean nitrate and dissolved oxygen concentrations ( $\pm 1$  standard deviation). The resultant plot shows a systematic increase in nitrate concentrations at mid-water depths ‘down’ the Atlantic and ‘up’ the Pacific, and an opposite trend for oxygen. These spatial patterns are the result of the time-integrated aerobic decomposition of organic matter along known pathways of deep water circulation.

concentrations of inorganic nutrients and low microbial biomass (Figure 8). The euphotic zone has been described as a ‘two-layer’ habitat with an uppermost light-saturated, nutrient-limited layer (0–100 m) which supports high rates of primary productivity and respiration, and a lower (>100 m) light-limited, nutrient-sufficient layer. A region of elevated chl *a*, termed the Deep Chlorophyll Maximum Layer (DCML), defines the boundary between the two

layers (Figure 9). The DCML in the NPSG results from photoadaptation (increase in chl *a* per cell) rather than enhanced phototrophic biomass; this can also be seen in the near-surface ‘enrichment’ of chl in winter when light fluxes are at their seasonal minimum (Figure 9).

Previously considered to be the oceanic analogue of a terrestrial desert, the NPSG is now recognized as a region of moderate primary productivity

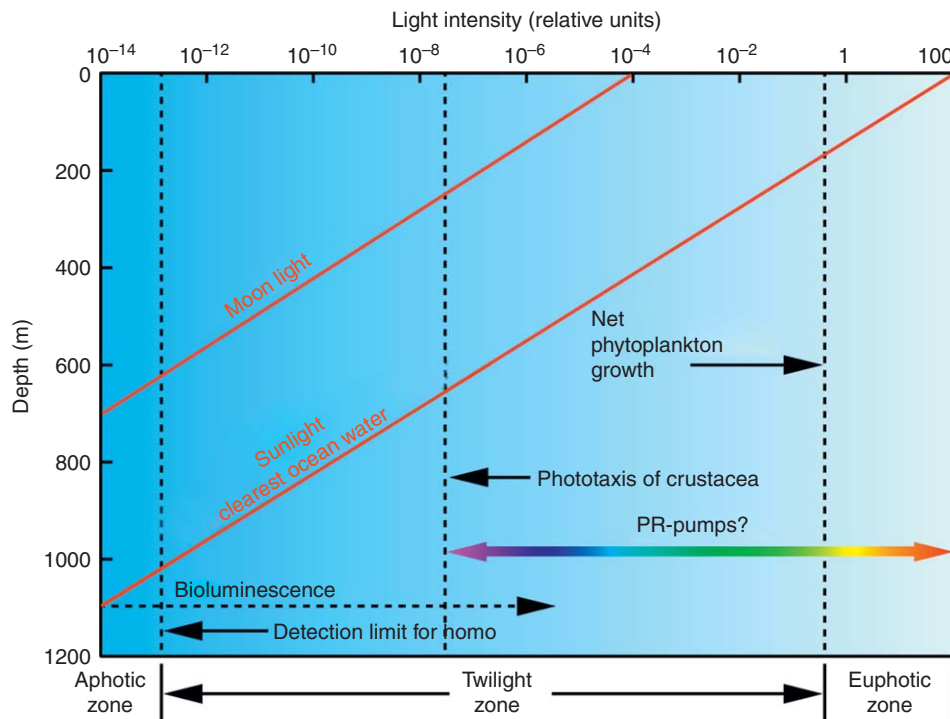
**Table 3** Conditions for microbial existence in the three major habitats at Station ALOHA in the North Pacific Subtropical Gyre

Habitat	Depth range (m)	Conditions
Euphotic zone (nutrient-limited)	0–200	<ul style="list-style-type: none"> <li>• high solar energy</li> <li>• high DOM</li> <li>• low inorganic nutrients, trace elements, and organic growth factors</li> </ul>
Mesopelagic (twilight) zone (transition)	200–1000	<ul style="list-style-type: none"> <li>• low solar energy</li> <li>• decrease in reduced organic matter with depth</li> <li>• increase in organic nutrients and trace elements with depth</li> </ul>
Abyssal zone (energy-limited)	>1000	<ul style="list-style-type: none"> <li>• no solar energy</li> <li>• low DOM</li> <li>• high inorganic nutrients and trace elements</li> </ul>

(150–200 g carbon m<sup>-2</sup> year<sup>-1</sup>), despite chronic nutrient limitation. Furthermore, based on data from the HOT program it appears that the rates of primary production have increased by nearly 50% between the period 1989 and 2006 due in part to enhanced nutrient delivery

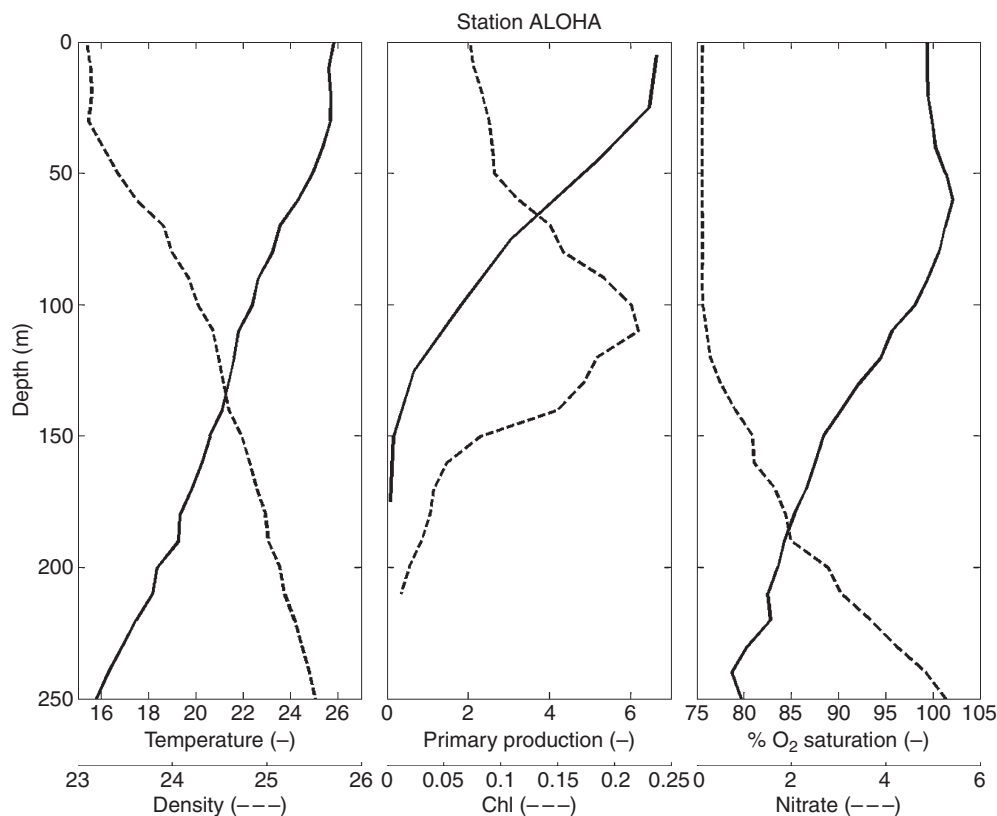
resulting from climate controls on habitat structure and function.

At Station ALOHA the light-supported inorganic carbon assimilation extends to 175 m, a depth that is equivalent to the 0.05% surface light level (~20 mmol quanta m<sup>-2</sup> day<sup>-1</sup>). Most of the light-driven inorganic carbon assimilation (>50%) occurs in the upper 0–50 m of the water column (Figure 8), a region of excess light energy (>6 mol quanta m<sup>-2</sup> day<sup>-1</sup>). In addition, chemoorganoheterotrophic microbial activities are also greatest in the upper 0–50 m. However, unlike photolithoautotrophic production (where light is required as the energy source and inorganic carbon is assimilated for growth), the metabolism of chemoorganoheterotrophs is not dependent on light energy so it continues, albeit at a reduced rate, well into the twilight zone and beyond. Recently, it has been observed that ‘heterotrophic production’ at Station ALOHA is enhanced by sunlight, suggesting the presence of microorganisms using light and both inorganic and organic substrate (photolithoheterotrophic) or light and organic substrates (photoorganoheterotrophic) to support their metabolism, or both. Several possible pathways for solar energy capture and carbon flux potentially exist in the euphotic zone at Station ALOHA, and we are just beginning to establish a



**Figure 7** Schematic representation of the distribution of light in open ocean marine habitats. The X-axis displays light intensity (on a log<sub>10</sub> scale in relative units) and the Y-axis is water depth. The euphotic zone where net photosynthesis can occur extends to a depth of ~150–200 m but sunlight can be detected by mesozooplankton (crustacean and fish) to depths of 800 m or more. The dark adapted human eye can detect even lower light fluxes. Proteorhodopsin proton pumps that have recently been detected in marine bacteria may also be able to use light but this is not yet confirmed. Moonlight, in contrast, is ~10<sup>-4</sup> as bright as sunlight, but can also be detected by marine organisms and, perhaps, microbes. Bioluminescence, light production via cellular metabolism that can be found in nearly all marine taxa including microorganisms, is found throughout the water column even in the ‘aphotic’ zone.





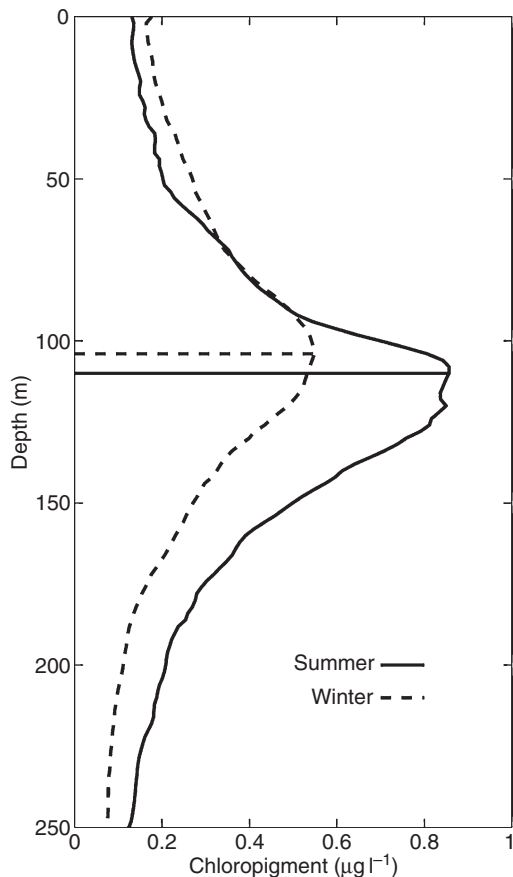
**Figure 8** Typical patterns of the vertical distributions of selected physical and biological parameters at Station ALOHA in the NPSG. The base of the euphotic zone, defined here as the depth where primary production is equal to zero, is ~175 m. Units are: temperature ( $^{\circ}\text{C}$ ), density (shown as density anomaly;  $((\text{density g cm}^{-3}) - 1.000) \times 1000$ ), primary production ( $\text{mg C m}^{-3} \text{ day}^{-1}$ ), chlorophyll ( $\text{mg m}^{-3}$ ), nitrate ( $\mu\text{M}$ ), and  $\text{O}_2$  (% of air saturation). Compiled from the HOT program database (<http://hahana.soest.hawaii.edu>).

comprehensive understanding of these processes, their roles and controls, and the diversity of microbes supporting them in the pelagic ecosystem.

As described earlier, physical and chemical depth gradients in the water column affect the vertical distribution of microbial assemblages and their metabolic activities. Furthermore, at a macroscopic scale we can assess how each depth horizon is affected by different temporal patterns of variability, which, in turn, influence the microbial environment. For example, in the upper euphotic zone the variability in solar radiation due to cloud coverage and changes in day length associated with the seasonal solar cycle can affect the rates of photosynthesis. In this habitat, far removed from the upper nutricline (the depth at which nutrient concentrations start to increase), the dynamics of microbial processes will be controlled mainly by the rates of solar energy capture and recycling of nutrients through the food web. Furthermore, upper water column mixing rates also contribute significantly to the variability in the light environment. However, if the variability has a high frequency relative to the cell cycle, then microbes integrate the signal because the energy invested in acclimation may be greater than that gained

by maximizing photosynthetic and photoprotective processes along the variability (light) gradient.

Between the base of the mixing layer and the top of the nutricline, the microbial assemblage resides in a well-stratified environment that is nevertheless still influenced by variability in light. Although mixing does not play a significant role in this habitat, unless a deep wind- or density-driven mixing event occurs, the vertical displacements of this stratified layer as the result of near-inertial period ( $\sim 31$  h at the latitude corresponding to Station ALOHA) oscillation forces may introduce strong day-to-day variability in the light availability and photosynthetic rates (Figure 10); these vertical motions can affect the short-term balance between photosynthesis and respiration. The variability in solar irradiance described above propagates into the lower euphotic zone, penetrating into the upper nutricline. But the apparent presence of excess nutrients relative to the bioavailable energy that can be derived through photosynthesis in this region indicates that light is the limiting factor supporting microbial activity. For this reason, day-to-day variations, as well as the seasonal cycle of solar irradiance in this layer may trigger successional patterns in the microbial



**Figure 9** Vertical distributions of chloropigments (chlorophyll plus pheophytin) determined from *in vivo* fluorescence measurements and bottle calibrations. These graphs show average distributions at Station ALOHA for summer (June–Aug) versus winter (Dec–Feb) for 1999 showing and documenting changes in both total concentration of chloropigments at the surface and at the depth of the Deep Chlorophyll Maximum Layer (DCML). Both of these seasonal differences are caused primarily by changes in light intensity.

assemblage, and lead to pulses of organic matter export into the deeper regions of the ocean.

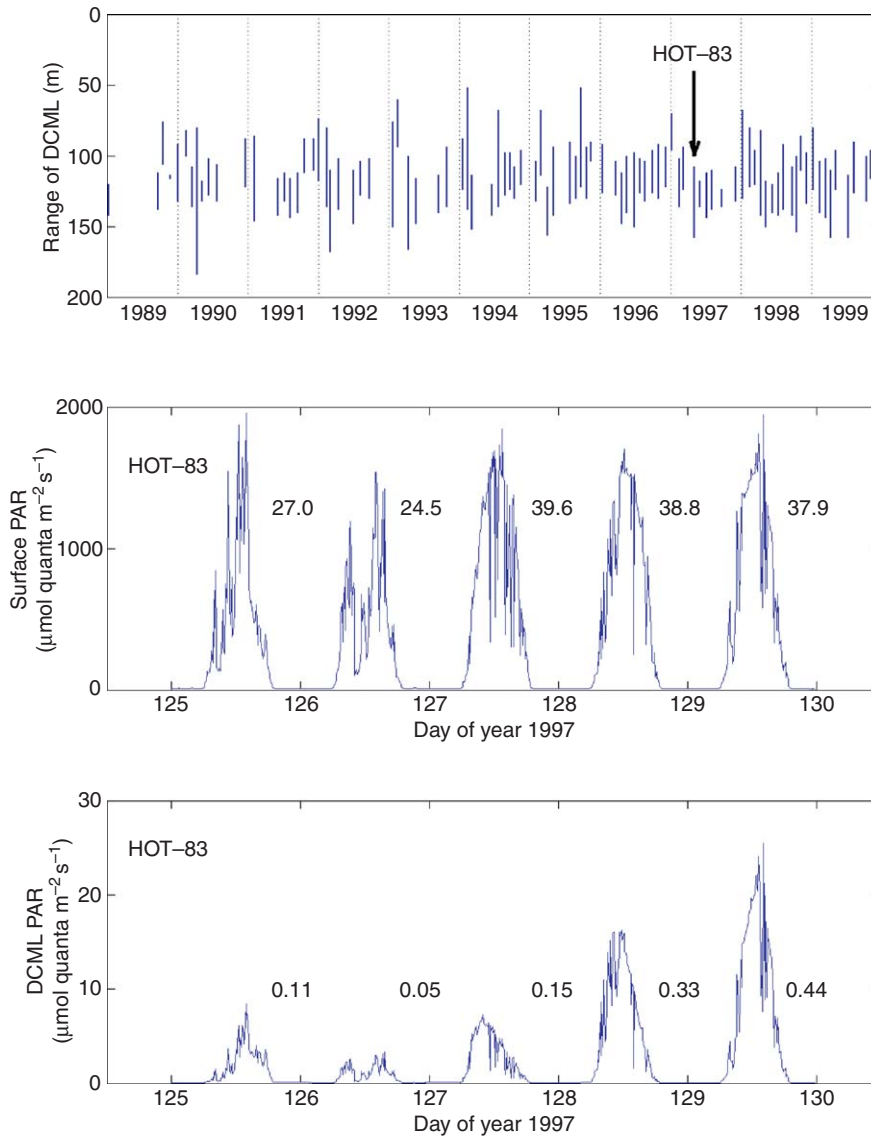
At Station ALOHA, as well as in most oceanic regions, the gravitational flux of particles formed in the euphotic zone represents the major source of energy that links surface processes to the deep sea. In addition, these sinking organic particles represent energy- and nutrient-enriched microhabitats that can support the growth of novel microbial assemblages. The remineralization of particles with depth follows an exponential decay pattern indicating that most of the organic matter in these particles is respired in the upper layer below the euphotic zone. If the quality and quantity of organic rain was constant, we would expect to observe stable layers of microbial diversity and activity with depth. However, the long-term records of particle flux to abyssal depths at Station

ALOHA suggest that, during certain periods of the year, this flux increases significantly, representing potential inputs of organic matter into these deep layers driven by changes in upper water column microbial processes. Microscopic analysis of these organic matter pulses at Station ALOHA reveal that their composition is dominated by diatoms. These photolithoautotrophic microbes produce an external siliceous skeleton that can act as strong ballast when the cells become senescent.

Several mesoscale physical processes have been observed that can modify the upper water column habitat at Station ALOHA, triggering an increase in the relative abundance of diatoms in surface waters and subsequent cascade of ecological processes. The passage of mesoscale features, such as eddies and Rossby waves, can shift the depth of nutrient-rich water relative to the euphotic zone, leading to a possible influx of nutrients into the well-lit zone that can last from days to weeks. This sustained nutrient entrainment can alter the microbial size spectrum, in favor of rapidly growing, large phytoplankton cells (usually diatoms), resulting in a bloom. In addition, eddies can trap local water masses and transport microbial assemblages for long distances.

A second mechanism triggering changes in the microbial community appears to occur during summer months at Station ALOHA, when the upper water column is warm and strongly stratified. Under these conditions,  $N_2$ -fixing cyanobacteria, sometimes living in symbiosis with diatoms, aggregate in surface waters and provide an abundant supply of reduced nitrogen and organic matter to the microbial community. Although it is still not clear what triggers these summer blooms, *in situ* observations suggest that they significantly alter the structure and metabolic activity of the microbial assemblage.

Finally, the mixing layer can periodically penetrate to a depth where it erodes the upper nutricline and delivers nutrients to the surface waters, while mixing surface-dwelling microbes into the upper nutricline. This deepening of the mixing/mixed layer can be driven by sudden events such as the development of a severe storm or the cooling of surface waters by the passage of a cold air mass. And, although each of these three mechanisms can lead to the entrainment of nutrients into the euphotic zone, they generate different microbial responses and interaction. For example, while the first two mechanisms do not involve a change in stratification, the third mixes the water column temporarily erasing the physical, chemical, and biological gradients that had existed before the event. Furthermore, while the passage of eddies and Rossby waves introduce nutrients into the base of the euphotic zone, affecting primarily the microbial populations inhabiting the upper nutricline, summer blooms have their strongest effect in the microbial assemblages residing in the upper few meters of the water column. Nevertheless, all these mechanisms appear to generate pulses of particulate organic matter rain that enhance the availability of



**Figure 10** Effect of isopycnal vertical displacements in accounting for day-to-day variability of Photosynthetically Available Radiation (PAR) at the DCML at Station ALOHA: (Top) Observed minimum and maximum depth range distribution of the DCML for each HOT cruise based on continuous fluorescence trace profiles obtained from 12 CTD casts deployed over a 36-h sampling period. (Center) Surface PAR measured at the HALE ALOHA mooring location during HOT-83 (5–9 May 1997). (Bottom) Estimated PAR at the DCML based on the vertical displacement of the DCML, surface PAR, and assuming  $k_{\text{PAR}} = 0.04 \text{ m}^{-1}$ . Daily integrated PAR values (in  $\text{mol quanta m}^{-2} \text{ day}^{-1}$ ) are displayed next to each light cycle in (Center) and (Bottom). These day-to-day variations in light caused by inertial period oscillations of the DCML and variations in surface PAR due to clouds are certain to have significant effects on rates of *in situ* photosynthesis. Reproduced from Karl DM, Bidigare RR, and Letelier RM (2002) Sustained and aperiodic variability in organic matter production and phototrophic microbial community structure in the North Pacific Subtropical Gyre. In: Williams PJ, le B, Thomas DR, and Reynolds CS (eds.) *Phytoplankton Productivity and Carbon Assimilation in Marine and Freshwater Ecosystems*, pp. 222–264. London: Blackwell Publishers.

ephemeral microenvironments, fuel the deeper microbial layers, and carry microbes to depth.

In addition to mesoscale events and seasonal cycles that seem to support small transient changes in the microbial community structure and function, variability at longer time scales (interannual to decadal) may shift the taxonomic structure of the microbial community. For example, there is evidence suggesting that a significant shift in the

dominance of phototrophic taxa may have taken place in the NPSG as a result of changes in ocean circulation and wind forcing during the 1970s. More recently, changes in the stability of the upper water column since the 1997–98 El Niño event may have also triggered long-term changes in the phototrophic community structure.

Ultimately, these long-term habitat changes are the result of processes taking place over a broad range of

scales propagating into the habitat experienced by a microbe. In this context, the advent of novel molecular tools such as metagenomic, proteomic, and transcriptomic analyses has provided an unprecedented opportunity to infer the diversity and biogeochemical relevance of microhabitats via the characterization of the genes being expressed in the environment. These new tools may help us better explore how physical and biological processes, by affecting the spatial and temporal distribution of these habitats, shape the microbial diversity and metabolism in the sea. However, understanding how microbial assemblages in different oceanic habitats may evolve over time in response to climate change will require not only a characterization of the microbes' response to physical and chemical changes, but also the development of an understanding of how interactions among microbes contribute to the plasticity and resilience of the microbial ecosystem in the marine environment.

### Summary and Prospectus

All marine habitats support diverse microbial assemblages that interact through a variety of metabolic and ecological processes. The characteristics and dynamics of marine habitats determine the composition, structure, and function of their microbial inhabitants. Many microbial habitats (i.e., microhabitats) are cryptic, ephemeral, and difficult to observe and sample; the spatial and temporal domains of these environments are poorly resolved at present. The changing ocean will lead to different and, probably, novel marine habitats that will select for new microbial assemblages. Future ecological research should focus on the relationships among climate, habitat, microbes, and their individual and collective metabolic function. These comprehensive studies demand coordinated, transdisciplinary field programs that fully integrate physical and chemical oceanography with theoretical ecology into the wonderful world of marine microbes.

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See also: Algal Blooms; Aquaculture; Archaea (overview); Regulation of Carbon Assimilation in Bacteria; DNA Sequencing and Genomics; Deep-Sea Hydrothermal Vents; Ecology, Microbial; Food Webs, Microbial; High-

Pressure Habitats; Horizontal Transfer of Genes between Microorganisms; Low-Nutrient Environments; Metabolism, Central (Intermediary); Nitrogen Cycle; Phosphorus Cycle; Photosynthesis: Microbial; Picoeukaryotes; Regulation of Carbon Assimilation in Bacteria; Sediment Habitats, including Watery; Stable Isotopes in Microbial Ecology

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- <http://hahana.soest.hawaii.edu> – Microbial Oceanography, Hawaii
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