MARINE ECOLOGY

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Summary: The Ocean Ecosystem

The ocean is the largest biome on the biosphere, and the place where life first evolved. Life in a viscous fluid, such as seawater, imposed particular constraints on the structure and functioning of ecosystems, impinging on all relevant aspects of ecology, including the spatial and time scales of variability, the dispersal of organisms, and the connectivity between populations and ecosystems. The ocean ecosystem contains a greater diversity of life forms than the terrestrial ecosystem, even though the number of marine species is almost 100-fold less than that on land, and the discovery of new life forms in the ocean is an on-going process. Marine food webs contrast with terrestrial food webs in the higher number of trophic levels, and the dominance of heterotrophic biomass, particularly in planktonic, unproductive ecosystems. In addition, marine photosynthesis is restricted to the upper skin of the ocean (100 m), whereas most of the ocean volume is occupied by a dark ecosystem, dependent on organic matter settling from the upper, illuminated layer or exported laterally from the coastal shelf. Most (75 percent of the surface) of the ocean is occupied by oceanic deserts, where the supply of nitrogen, the main driver of biological production in the ocean, is limited by restricted

mixing of the upper, illuminated waters with deeper, nutrient rich waters. In contrast, coastal ecosystems, particularly those dominated by larger plants (seagrass, macroalgae, mangroves) are highly productive, and produce organic matter in excess of the local requirements, which can either be stored permanently in the sediment, sequestering carbon dioxide from the atmosphere, or can be exported to other, deficient, ecosystems. Widespread habitat destruction in the coastal zone, along with excessive nutrient inputs to the coastal zone, overfishing, and human alteration of the global climate are leading to major changes in marine ecosystems. These changes jeopardize the services society receive from marine ecosystems, including food supply, climate, and regulation of the planet's biogeochemical system, as well as cultural and leisure values.

1. Introduction: The Sea as an Ecosystem

If seen from space, it is odd that our planet's name is Earth, for it should be planet Ocean, since this would be the main feature evident to a hypothetical extraterrestrial observer, and also the main distinctive feature of our planet in comparison to its companion planets in the solar system. The ocean is also the cradle of life, where the earliest organisms evolved, and is, therefore, the primogenial ecosystem in the planet. Moreover, as life extended in the ocean, oxygen produced by photosynthesis eventually altered the earth's atmosphere and the associated biogeochemical conditions, rendering the land amenable to support life as well. The ocean as an ecosystem has a distinct three-dimensional configuration, when compared to land, since life occurs throughout the extensive oceanic volume of $1{,}348 \times 10^6$ km^3, due to the greater viscosity and the presence of nutrients and organic matter throughout the entire volume of the ocean. The habitat available to support life in the ocean ecosystem is, therefore, about 300 times larger than that available to support life on land, where this develops as a thin (0–50-m tall) crust on the land surface in contrast to the presence of life throughout the 11,000-m depth range of the ocean water column and sediments.

The ubiquity of life in the ocean is, however, a recent discovery to science. Although the study of marine biology has a long tradition, since Aristotle summarized the knowledge in classical Greece, the exploration of life in the sea developed as an articulated venture in the nineteenth century. Until the late 1800s marine life was believed to be confined to the upper 300 m in the ocean, and the dark ocean (i.e., that extending down to the ocean floor), was believed to be azoic. One of the main goals of the oceanographic expeditions in the late nineteenth century, such as the *Challenger* expedition, was to probe the existence of life in the dark ocean, initiating an era of exploration of the sea that still continues. The discovery of life in the ocean is still an on-going process, with the discovery of a new invertebrate phylum, the *Pogonophora*, in the sea; the discovery of the benthic fauna in the deep ocean; the discovery of the rich life around hydrothermal vents, with its unique metabolic pathways; and the discovery a decade ago of *Prochloroccocus*, perhaps the oldest and smallest group of oxygenic phototrophs in the ocean, where it is one of the main primary producers. The ocean still conceals discoveries yet to be made, not only within the smallest organisms, but also within some large ones, including giant squids, which have never been observed alive, or large, deep-water sharks. Hence, the discovery of life itself and the diversity of life forms in the ocean lags well behind the inventory of life forms and species on land, leading to an insufficient understanding of biodiversity patterns in the ocean.

2. Marine Biodiversity and Marine Habitats

The evolution of life forms in the sea has a much longer history than that on land, and, as a result, the diversity of life forms in the sea is far greater than that on land. The sea contains forty phyla, of which fifteen are exclusively marine, whereas there is only one phylum restricted to life on land. The diversity of animal life forms is particularly large in the ocean, where thirty-four of the thirty-seven animal phyla are present. Yet, the number of known marine animal species appears to be only 2 percent of that on land, despite the greater space available for life in the ocean. The number of multicellular species seems to be in the order of 200,000 in the sea, compared to about 12 million on land (Table 1). Most (about 96 percent) of the marine species inhabit the bottom of the sea, and conform benthic communities, with most of the species inhabiting in the littoral and coastal zone, particularly those in tropical latitudes, with only 0.5 percent of the species present in the abyssal (> 6,000 m) ocean. Marine organisms range over 10^8-fold in size, from the smallest bacteria (< 0.5 µm) to the largest whales.

Oceans		Land	
Phylum	**Number of species (estimated)**	**Taxa**	**Number of species (estimated)**
Porifera	9 000	Insects	10 000 000
Cnidaria	9 000	Acarid	750 000
Nematoda	35 000	Spiders	170 000
Anelida	15 000	Nematods	1 000 000
Arthropoda	37 000	Molluscs	20 000
Mollusca	29 000	Other	100 000
Bryozoa	15 000		
Chordata	15 000		
Others	14 000		
TOTAL ANIMALS	178 000		12 040 000
Vascular plants	< 100		300 000
Pluricellular algae	7 000		
TOTAL	185 100		12 340 000

Table 1. The estimated number of species in different phyla on land and in the ocean

Yet, most of the plant and animal species on land are contained within a single group each (angiosperms and arthropods, respectively), so that much of the plant and animal diversity on land represent but the reiteration of a single, highly successful, growth plan. In fact, the speciation of the two dominant groups of animals (insects) and plants (angiosperms) are closely linked through co-evolutionary processes, which have not been found to occur to similar extents in the ocean.

The process of speciation has been hypothesized to be set by the space available to life, the energy available to support it, and the stability required to allow speciation. All of these factors could be considered to be at least as high, if not higher, in the ocean as on land, and yet the number of species seems to be smaller than on land. In fact, the number of species in the ocean is still highly uncertain, particularly since the ocean floor remains poorly explored. Hence, the present estimates of about 200,000 species of multicellular organisms could be significantly reviewed upwards in the future. An indication that the present knowledge on the oceanic biodiversity is still very poor lies in the fact that two new phyla have been described since 1980, whereas new findings on land are placed at a much lower taxonomic level. The knowledge of marine bacteria is even poorer, and < 5 percent of the bacteria present in any one sample of seawater have been named. Active bacteria have been found in extreme habitats, such as hydrothermal vents and deep (> 100 m) sediment layers.

Whether the distribution of species in the ocean follows some of the large-scale patterns derived for land biodiversity remains uncertain. There is evidence, for some taxa, that species diversity is greatest towards the tropics. However, this pattern, evident for taxa such as corals, mangroves, and seagrasses, does not represent a latitudinal gradient *per se*, but is confounded by the presence of a nucleus of high species richness in the Indo-Pacific region, with species diversity declining in all directions with distance from this hot spot. The species richness, for any one tropical group, in the Indo-Pacific region is two- to seven-fold higher than that in any other tropical marine region, and has been attributed to the relative stability of this area since the formation of the Tethys Ocean. The large scale patterns in marine, particularly benthic, biodiversity are explained by changes in the configuration of the oceans resulting from plate tectonics. Indeed, relatively recent events, such as the closure of the Panama isthmus, have resulted in active speciation and the development of vicariant species.

The major habitat division in the marine ecosystem is between benthic (or associated to the sea floor) and pelagic (suspended in the water column) ecosystems. Depending on depth, both benthic and pelagic habitats can be divided into a series of layers, including the photic layer, where sufficient light to support photosynthesis reaches, and that extends between a few meters to 200 m in the clearest marine waters in the central gyres of the subtropical ocean. The mesopelagic layer extends from the bottom of the photic layer to the bottom of the permanent thermocline at about 1,000 m depth. The bathypelagic zone extends down to the bottom of the sea, and is often differentiated into bathyal and abyssal zone by the depth of the 4°C layer (at about 2,000 m depth), which is an important boundary for many organisms, and a deeper layer (> 6,000 m), the hadal zone.

The photic zone in the coastal zone encompasses the littoral zone, characterized by the presence of benthic primary producers of various forms depending on the substrate (muddy, sandy, or rocky), and the mesopelagic zone in the continental margins, which encompasses the shelf and slope areas. A further habitat in the littoral zone is the intertidal zone, where the benthic habitat is temporarily exposed to air during low tides, and which is often inhabited by specialized fauna and flora, either partially tolerant to exposure to air or, conversely, partially tolerant to immersion in seawater (e.g., most mangrove and salt marsh vegetation). The benthic habitat contains infauna, which live inside the sediments, suprafauna, which live on the sediments, and epifauna, which live on the surfaces of benthic animals (e.g., coral reefs, bivalve shells) or plants (e.g., seagrass and macroalgae).

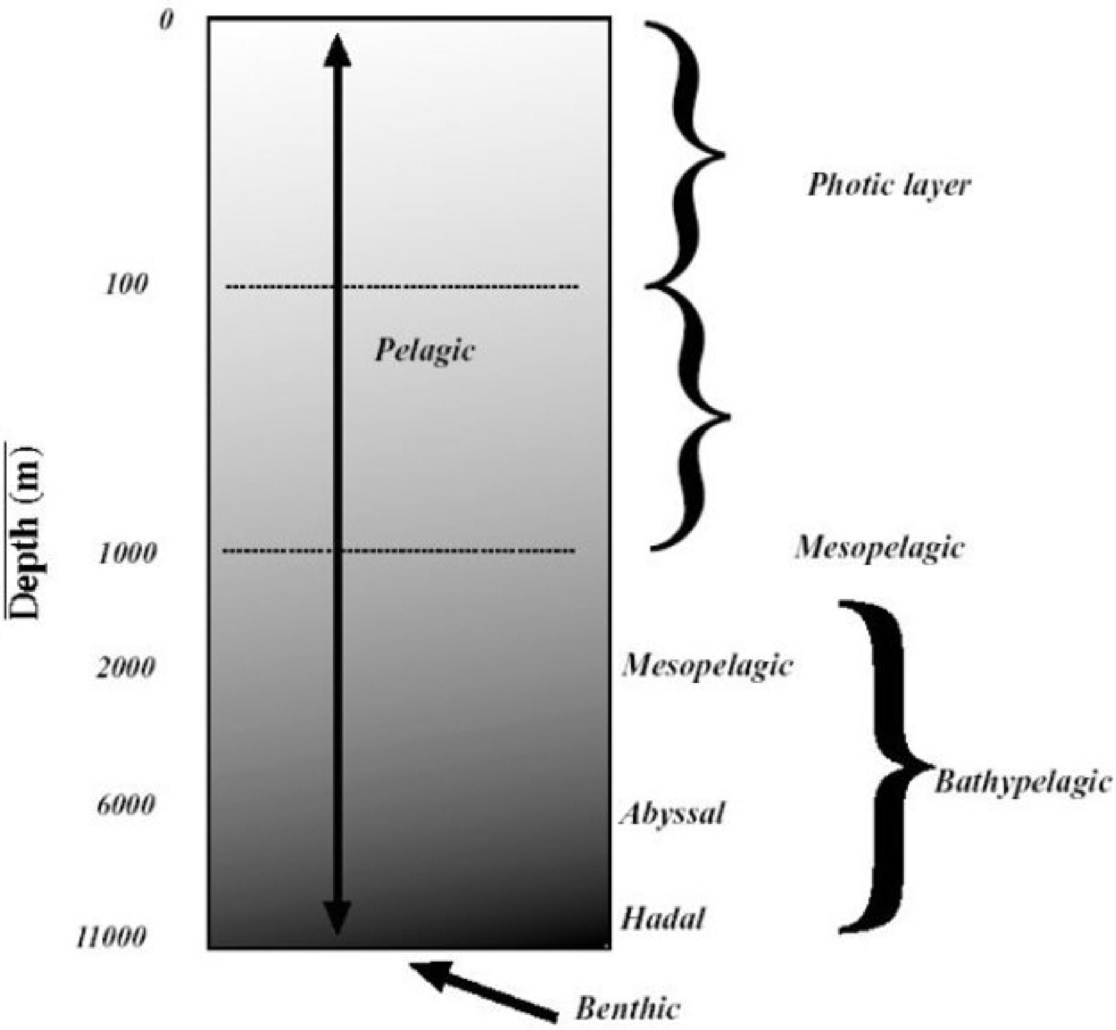

Figure 1. The different habitats present in the ocean

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Biographical Sketch

Carlos M. Duarte (Lisbon, 1960) is Research Professor with the Instituto Mediterráneo de Estudios Avanzados (CSIC-UiB) in Esporles, Majorca, Spain, where he presently conducts research on a broad range of subjects within marine ecology, including planktonic and benthic ecology in tropical, temperate, and polar ecosystems, as well as global ecology. Dr Duarte received his Ph.D. degree, on Limnology, from McGill University (Montreal, Canada, 1987), and after a brief postdoctoral position in the University of Florida (Gainesville, Florida, USA), worked as postdoctoral fellow for two years in the Instituto de Ciencias del Mar in Barcelona (Spain), where he took a permanent position as a research scientist in 1989, to later work as a staff scientist at the Centro de Estudios Avanzados de Blanes until 1999, when he took his present position as senior scientist in Majorca. Dr Duarte's research has particularly emphasized comparative aspects on the ecology of marine autotrophic organisms, food web processes, and ecosystem metabolism. Dr Duarte's present research has broadly contrasting scenarios, such as the Mediterranean, the North Sea, the Norwegian Sea, South-east Asia, Australia, North America, and Antarctica. Author of over 200 scientific articles and about a dozen book chapters, and co-author of *Seagrass Ecology* (Cambridge University Press, 2000), Dr Duarte is now member of the editorial committee of eight international journals. Dr Duarte's contribution to Marine Ecology was recognized by 2001's G. Evelyn Hutchinson Award from the American Society of Limnology and Oceanography.