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PINNIPEDS

See **MARINE MAMMAL OVERVIEW**

PLANKTON

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

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

Although horizontal movement of plankton at kilometer scales is passive, the metazoan zooplankton nearly all perform vertical migrations on scales of 10s to 100s of meters. This depth range can take them from the near surface lighted waters where the phytoplankton grow, to deeper, darker and usually

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

The plankton can be subdivided along functional lines and in terms of size. The size category, picoplankton (0.2–2.0 µm), is approximately equivalent to the functional category, bacterioplankton; most phytoplankton (single-celled plants or colonies) and protozooplankton (single-celled animals) are nano- or microplankton (2.0–20 µm and 20–200 µm, respectively). The metazoan zooplankton (animals, the 'insects of the sea') includes large medusae and siphonophores several meters in length. Size is more important in oceanic than in terrestrial ecosystems because most of the plants are small (the floating seaweed, *Sargassum*, being the notable exception), predators generally ingest their prey whole (there is no hard surface on which to rest prey while dismembering it), and the early life stages of many

types of zooplankton are approximately the same size as the larger types of phytoplankton. Therefore, while the dependence on light for photosynthesis is characteristic of the phytoplankton, the concepts of 'herbivore' and 'carnivore' can be ambiguous when applied to zooplankton, since potential plant and animal prey overlap in size and can be equivalent sources of food. Though rabbits do not eat baby foxes on land, analogous ontogenetic role-switching is very common in the plankton.

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

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

Zooplankton is typically more concentrated within the euphotic zone than in deeper waters, but because of sinking of detritus and diel vertical migration of some species into and out of the euphotic zone, organic matter is supplied and various types of zooplankton (and bacterioplankton and nekton) can be found at all depths in the ocean. An excep-

tion is anoxic zones such as the deep waters of the Black Sea, although certainly types of bacterioplankton that use molecules other than oxygen for their metabolism are in fact concentrated there.

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

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

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

See also

Bacterioplankton. Continuous Plankton Recorders. Gelatinous Zooplankton. Phytoplankton Blooms. Protozoa, Planktonic Foraminifera. Small Scale Physical Processes and Plankton Biology. Zooplankton Sampling with Nets and Trawls.

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PLANKTON AND CLIMATE

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Introduction

Plankton has two roles with respect to climate: first as an indicator of climate change in present day populations and in the fossil record and second as a factor contributing to climate change through, for example, its role in the CO₂ cycle, in cloud formation via dimethylsulfide (DMS) production, and in altering the reflectivity of sea water as a component of suspended particulate matter. Current research on both the contribution of plankton to climate change and its role as an indicator of change are central to predicting potential scenarios that may occur in the future at a time when global mean temperatures are predicted to rise at an unprecedented rate by 1.5–6°C within the next 100 years.

Plankton as an Indicator of Climate Change

Growth of phytoplankton is dependent on the degree of mixing/stability of the water column, light intensity, and input of nutrients. All these variables in turn are governed by wind strength/direction/frequency, cloudiness, precipitation, and other factors that exert a strong control on the top 100 m of the water column through which light may penetrate in clear oceanic conditions. As light is rapidly attenuated by absorption and reflection, most primary production occurs in the upper 40 m of the water column or in the pycnocline where nutrients are more available. In turbid shelf seas light penetrates to shallower depths. Many of these factors also impact zooplankton, which process primary production and are the food source for fish and other

higher trophic levels. Plankton is thus an integrator of a wide range of hydrometeorological factors and it is likely that changes in abundance and variations in community structure may act as indicators of climate change. It is on this premise that the first section of this paper is predicated.

Fossil Plankton and Climate Change

Many planktonic organisms, especially microplankton, have hard parts (e.g. carbonate, silicate) that are deposited each year in large numbers on the bottom of the oceans. Their spatial distribution and volume have been shown to be representative of the productivity of overlying ecosystems and circulation at the time of deposition. For example, there is a long history of the application of planktonic foraminifera, coccolithophores, and dinoflagellate cysts to interpret the changing climate of the oceans as recorded in deep-sea cores, especially in the Quaternary and Holocene periods of the last 4 million years. The Holocene includes the period since the end of the last glaciation, approximately 10 000 years before present. The results obtained from core profiles together with isotopic information from the planktonic shells provide evidence for alternating cold and warm periods and changing patterns of ocean circulation. They indicate that marked reductions occurred in the thermohaline circulation during glaciated periods. In warmer periods such as the Holocene larger quantities of dense, cold, and salty water sink at convection sites in Arctic seas and spread out across the bottom of the deep ocean to be replaced at the surface by a compensatory counterflow of warm and salty water. It is this mechanism, as part of what is known as the 'global conveyor belt', that helps insure that the climate of Europe is much warmer than the equivalent latitude on the western side of the Atlantic. Combined with information from other sources such as the Greenland and Antarctic ice cores micropaleontological information also indicates that climate change may