dolphin-, seal-, and sea otter-watching supports an extensive network of tour operations around the world (**Figure 10**). Commercial fishermen 'exploit' pelagic dolphins in the tropical Pacific Ocean by using them to locate schools of tuna, and this can result in large numbers of dolphins being killed by accident.

See also

Baleen Whales. Marine Mammal Overview. Sea Otters. Seals. Sirenians. Sperm Whales and Beaked Whales.

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MARINE MATS

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The production of organic carbon in ocean surface waters and its subsequent transport to the seafloor is often referred to as the 'biological pump'. This biological pump is an important link in the global carbon cycle because phytoplankton use dissolved carbon dioxide (CO_2) gas to produce their organic matter. The concentration of dissolved CO_2 in surface waters is regulated by gas exchange with the atmosphere, so if carbon is utilized by phytoplankton which then sink, more CO_2 is drawn down from the atmosphere to compensate. One of the key steps in the biological pump is, therefore, the sinking of organic material from the surface waters – the faster organic material settles, the more efficiently the biological pump operates. Recent water column observations and complementary studies of deep-sea sediments have demonstrated that diatom mats and large diatoms are important, and in some cases, dominant contributors to the flux of biogenic material to the seafloor. Research on deep-sea sediment cores, in particular, has shown that such diatoms are locally abundant and may form thick, extensive deposits that have accumulated at rates exceeding 30 cm per 1000 years. These are exceptionally high for the pelagic realm and would normally occur only in areas of high sediment supply near continental margins or beneath coastal upwelling zones. A synergy between biological oceanography and paleoceanography has shown that these diatoms are key players in the biogeochemical cycles of carbon and silica and may be important regulators of global change.

Ecological Significance of Diatom Mats and Large Diatoms

In contrast to the relatively well studied, small, and rapidly reproducing diatoms that dominate primary production in coastal settings, the ecology of oceanic mat-forming and large ($>50\,\mu m$) diatoms is relatively poorly understood. These larger diatoms are the most widely distributed in the open ocean but had been regarded by biological oceanographers as typically occurring in very small numbers in oligotrophic (nutrient-depleted) surface waters. Such conditions dominate most of the central gyres of the ocean and also characterize some marginal seas such as the Mediterranean. These are the deserts of the oceans, but recent observations indicate that these deserts may bloom. An increasing body of field and experimental research on several species of large diatoms has shown that they possess a range of adaptations that allows them to exploit a unique ecological niche within the ocean. *Rhizosolenia* mats, for example, are able to regulate their buoyancy, migrating vertically tens or even hundreds of meters between nutrients (nitrate, phosphate, and silica) trapped at depth within the thermocline. Other species have adapted to grow in very low light conditions characteristic of nutricline depths (100 m) where they can draw on the essential nutrients and exploit mixing events caused by passing storms. A further adaptation is the coexistence of some diatom genera (including *Rhizosolenia* and *Hemiaulus*) with intracellular nitrogen-fixing symbionts that provide them with their essential chemical building blocks unavailable from the surrounding waters. Diatom mats may be up to several centimeters across and host a whole range of other organisms including smaller epiphytic diatoms, parasitic dinoflagellates, foraminifera, and small amphipods.

What Causes the Concentration and Mass Sinking of Diatom Mats and Large Diatoms?

How then are diatom mats and giant diatoms significant for flux to the seafloor? The existence of concentrated deposits of these diatom species in deep-sea sediments, including the giant *Ethmodiscus rex*, appeared to contradict the received view that they only occurred sparsely in the water column. Yet, until recently, there was only anecdotal historical evidence for the existence of substantial concentrations of these species.

Ocean Frontal Systems

In 1992 a breakthrough occurred, when an oceanographic experiment (the JGOFS–Joint Global Ocean Flux Study) in the eastern equatorial Pacific monitored extensive surface concentrations of the giant diatom *Rhizosolenia castrecaniae*. The surface concentrations were so intense that they were visible as ‘a line in the sea’ from the NASA Space Shuttle Atlantis. Parallel JGOFS seabed observations showed that these surface concentrations settled rapidly at rates of around 200 m per day over the 4000 m to the seabed. At the same time, Ocean

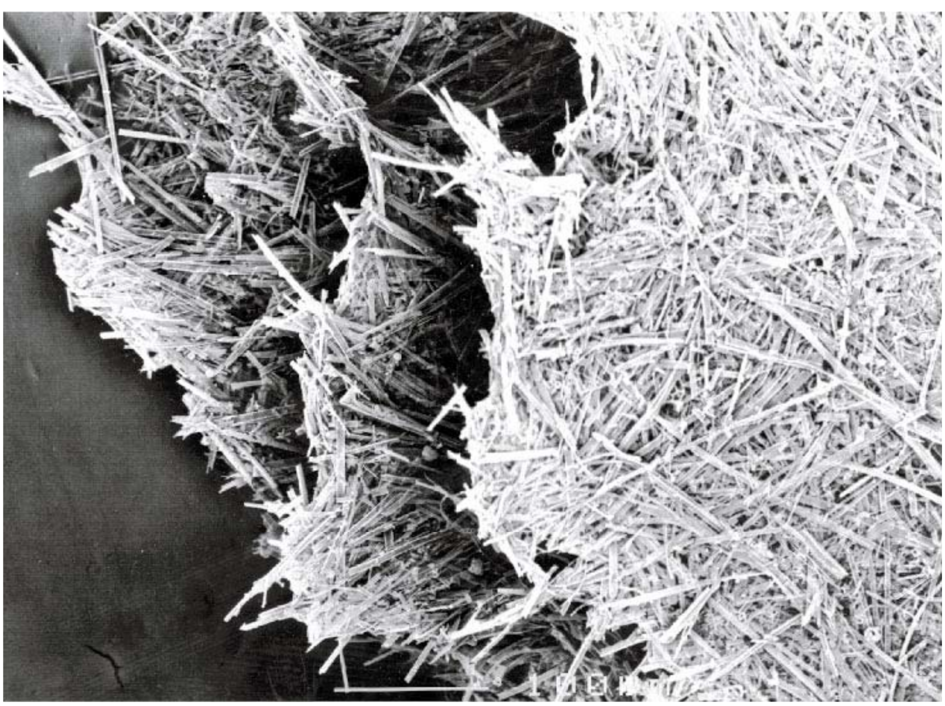

Figure 1 Mats of the needle-shaped diatom, *Thalassiothrix longissima*.

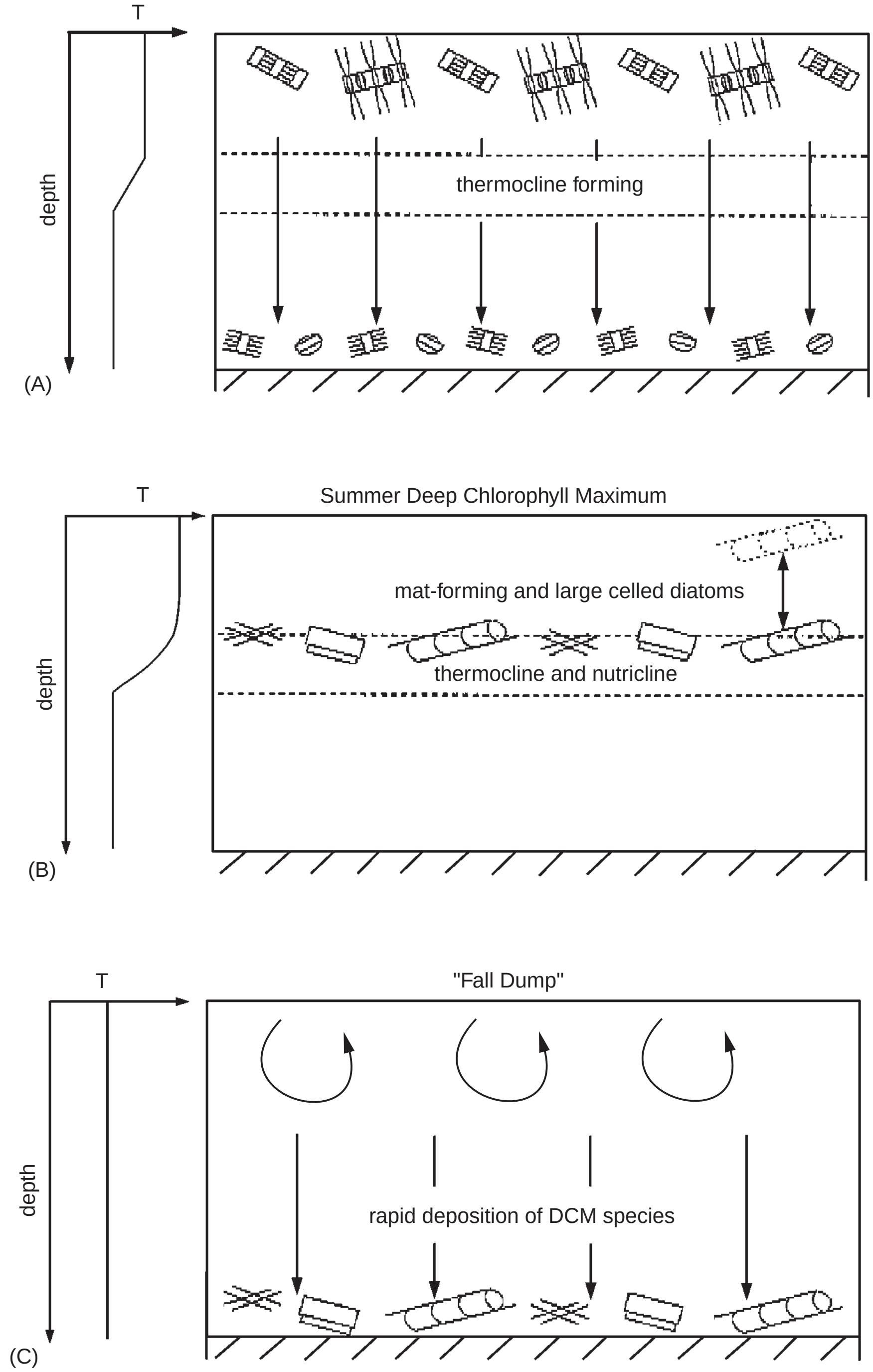

Figure 2 A cartoon representation of annual cycle of diatom production and flux. The autumn or fall dump of large and mat-forming diatoms is contrasted with the spring bloom or upwelling pulse. (A) Spring bloom of diatoms (or upwelling pulse) giving a growth episode lasting several days to a few weeks terminated with rapid aggregation and sinking. (B) Growth of diatoms in well-stratified summer conditions in deep chlorophyll maximum (DCM). Species adapted to low light conditions or to regulate buoyancy and migrate between nutrient-rich depths and bright surface. (C) Fall/winter mixing and resultant breakdown of stratification produces the ‘fall dump’; the mass sedimentation of diatoms which have grown during the period of summer stratification. (Modified from Kemp et al, 2000.)

Drilling Program cores, also from the eastern equatorial Pacific, revealed the presence of vast ancient deposits of the diatom *Thalassiothrix longissima*, a needle-shaped diatom that grows up to 4 mm in length and also forms tangled masses or mats (**Figure 1**). These layers that extend along the equator for > 2000 km record ancient surface concentrations of giant diatoms that settled to the seafloor between 4 and 15 Ma.

The 'Fall Dump'

As a result of sediment trap studies and work on ancient laminated marine sediments (the tree-rings of the oceans) a further explanation for mass flux for large and mat-forming diatoms has recently emerged (**Figure 2**). Most diatom production and flux was previously thought to be generated by small, rapidly growing diatoms in a spring bloom or upwelling pulse. However, a review of sediment trap studies and evidence from laminated sediments shows that large or mat-forming diatoms that grow in stratified waters in the summer and sediment massively when autumn or winter storms disrupt the water column may contribute as much or greater flux to the seafloor than the spring bloom. Ancient examples of this process are the Mediterranean sapropels, black layers whose high organic carbon content may be explained by the contribution from diatom flux.

See also

Carbon Cycle. Primary Production Distribution. Primary Production Methods. Primary Production Processes.

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MARINE MESOCOSMS

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Controlled experiments are the basis of the scientific method. There are obvious difficulties in using this technique when dealing with natural communities or ecosystems, given the great spatial and temporal variability of their environment. On land the standard method is to divide an area of ground, say a field, into a large number of equal plots. Then with a randomized treatment, such as nutrient addition, it is possible to replicate growth of plants and animals over a season.

It is apparent that this approach is not possible in the open sea because of continuous advection and dispersion of water and the organisms in it. Bottom-living organisms are an exception, especially these living near shore, so there have been a wide range of experiments on rocky shores, salt marshes, and sea grasses. But even there, the critical reproductive period for most animals involves dispersion of the larvae in a pelagic phase. Also these experiments require continuous exchange of sea water.

For the completely pelagic plants and animals, short-term experiments – usually a few days – on single species are used to study physiological responses. There can be 24-hour experimental measurements of the rates of grazing of copepods on phytoplankton in liter bottles. But for studies of