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 CO_2 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 occur abruptly within decades or shorter periods of time.

Long-Term Changes in the Plankton and Climate

In contrast to the fossil record, the longest regularly sampled planktonic time-series from the present day oceans is barely 50 years in length. Two of these data sets, the Continuous Plankton Recorder survey in the North Atlantic and the CalCOFI survey off the Californian coast in the Pacific, have both shown pronounced long-term declines in the abundance of the dominant components of the collections. Unfortunately the results of the two surveys cannot be directly compared as they are derived from different sampling methodologies. The Californian survey is based on a grid of parallel offshore transects with vertical zooplankton hauls down to 200 m and the CPR samples the plankton in the top 10 m on a band of silk. The measure of zooplankton taken in the Pacific survey is a volume displacement and the CPR analyses are based on counts of individual species. The Californian results have been attributed to basin-scale winter forcing of winds and the changes show an inverse relationship to sea temperatures in the upper 100 m. The results have not been updated since 1995 and it is not known for certain if they are linked to the regime shift in the north-east Pacific (see below) and/or associated with the Pacific Decadal Oscillation. The long-term trend in the CPR data has also been associated with a decline in the frequency of westerly winds, but does not appear to be linked to temperature changes. Other plankton data sets exhibit long-term change, including one from South Africa that shows an increasing trend. It is not known if the positive and negative trends shown by geographically separated time-series indicate a teleconnection link between different regions of the world's oceans and/or if the trends are a direct response to global warming. Parallel or opposite phase long-term changes in catches of industrial fish species such as sardines and anchovies have been observed from different regions around the world that may also be linked by teleconnections.

Remote Sensing and ENSO

Multispectral satellites such as the Nimbus CZCS and SeaWiFS have given a new insight into the complexity of the productivity of the world's oceans. Through the different absorbance properties of phytoplankton pigments it is now possible to map chlorophyll on a global scale, on an almost daily basis. Unfortunately many areas of the world are covered in cloud for much of the time so that monthly integrated maps are often produced as a standard product from the observations. These maps demonstrate regions of high productivity in the world, such as the northern North Atlantic and upwelling regions such as the Arabian Gulf. In his 1998 book on the *Ecological Geography of the Sea* Longhurst divided the oceans into 51 ecological provinces. He used satellite CZCS measurements of chlorophyll, with other information, to characterize the seasonal cycles of phytoplankton in each province. Satellite data provide a new source of information on which to evaluate future responses of the planktonic ecosystem to climate change.

The El Niño Southern Oscillation (ENSO) is one of a number of patterns in atmospheric circulation that have been defined for different regions of the world based on pressure gradients. The ENSO atmospheric phenomenon is Pacific wide with opposite effects to west and east and has a circum-global effect on regional climate, especially in tropical latitudes. Its impact on chlorophyll production in the central Pacific has been described using measurements taken by satellite color sensors. In the exceptionally strong 1997–98 El Niño year higher sea surface height with a much warmer and deeper stratified layer extended in a lens along the equator from Central America. Exceptionally low levels of chlorophyll and weaker winds were associated with this feature with a calculated fourfold reduction in the emission of CO_2 to the atmosphere. In the following summer, which had the opposite pattern, chlorophyll levels reached a record high.

The El Niño (boy child) phenomenon was named by Peruvian fishermen to describe the southern summer (Christmas) period (2–3 months) when winds are directed onshore, sea surface temperatures are warm and the fishery is poor. At these times offshore upwelling is reduced or ceases, limiting nutrient supply and leading to a substantial reduction in plankton growth. In El Niño years these conditions are exacerbated, lasting throughout the year or longer, leading to pronounced failures in the fishery with catches reduced by more than a fifth and mass mortalities of seabirds and marine mammals. Based on an anchovy and horse mackerel catch Peru is the largest exporter of fish meal in the world, as well as an important source of other fish products, so climatic events of this nature, through their impact on the plankton, have considerable economic impacts. The El Niño effect occurred in the past at approximately 7 year intervals, but appears to be increasing in frequency and intensity. Evidence from cores in the Gulf of California indicate that similar patterns of change have occurred over the last 2000 years – possibly as part of the decadal change equivalent of ENSO known as the Pacific Decadal Oscillation.

North Atlantic Hydrodynamics and the NAO

The North Atlantic Oscillation (NAO) has a similar importance (but longer timescale) to ENSO through its effect on the hydrodynamics of the North Atlantic. Evidence from physics and biology suggests that the circulation in the northern North Atlantic has changed in the recent period of high NAO index since approximately 1988. These changes are exhibited throughout the water column in upper, intermediate, and deep-water masses and appear to be linked to an alternating pattern between deep-water formation in the Greenland Sea and intermediate water in the Labrador Sea. The effects have been particularly pronounced in the Norwegian Sea, where Norwegian Sea deep water has shown a marked reduction so that the upper surface is now 600 m below the threshold to get out into the Atlantic through the ~ 800 m deep Faroe–Shetland Channel. The copepod *Calanus finmarchicus* overwinters in this cold deep water and the observed physical changes may be part of the reason why this species has declined so markedly in abundance in the northern North Sea.

Decadal productivity changes in the North Atlantic, which have implications for CO_2 fluxes, are correlated (regionally and temporally) with the NAO index. Since the early 1930s the 'phytoplankton colour index' recorded by the CPR survey has been used as an indicator of the overall abundance of phytoplankton. During the late 1980s and onwards there has been a considerable increase in phytoplankton color in certain areas of the north-east Atlantic and North Sea. Particularly high stepwise increases were seen after the mid-1980s in the northern and central North Sea and the central oceanic area between 52° and 58° N. An inverse pattern of change (decreasing trend) in phytoplankton color is seen in areas to the north and west of the British Isles.

With the exception of a region to the south of Iceland most of the areas in the north-east Atlantic have experienced higher temperatures and an increase in phytoplankton color from the late 1980s onwards. The north-west Atlantic has tended to experience colder surface temperatures but has also shown a decrease in phytoplankton color. These different regional responses can be partly explained by trends in the NAO. The NAO has positive correlations with sea surface temperature (SST) and phytoplankton color in the North Sea and some offshore regions in the north-east Atlantic, and negative correlations with SST and phytoplankton color in areas to the north and west of the British Isles. The different patterns seen are most likely a reflection of opposing responses to wind mixing, SST, and other hydro-climatic parameters influenced by trends in the see-saw effect of the NAO.

While a number of hydrographic variables show associations with the NAO index on short timescales and seem to have a passive response, it is thought that long-term cycles in the NAO are modulated by oceanic SST signatures which circulate around the Atlantic gyres and ultimately through the Atlantic's thermohaline circulation system. Further evidence for changes in circulation is seen from the plankton. Species more characteristic of warmer waters have increased and moved north in the eastern Atlantic, while the opposite has occurred in the west Atlantic where cold-water species have become more abundant and spread southwards.

Regime Shifts

The term 'regime shift' has been applied to the large decadal scale switches in the abundance, productivity, and composition of plankton and fish with associated environmental changes that have been observed in a number of sea areas around the world. Most of these geographically widespread and often step-like events appear to be associated with changes in regional hydrometeorological state, some are believed to be caused by extreme overfishing, while for others the forcing mechanisms are still unclear.

Major changes in the ecosystem of the western English Channel which started in the 1920s provide the first description of a regime shift. These events, known as the Russell Cycle, are recorded as a series of parallel step-like changes in fish, zooplankton, and nutrients. A major decline in macroplankton, herring stocks, and demersal fish larvae up to the late 1930s was followed by a system dominated by pilchards and small plankton with a partial reversal back to the conditions to the 1920s in the mid-1960s. The time-series on which this long series was characterized was unfortunately discontinued at a time (1988) when long-term monitoring was considered as poor science. This break in the series and the complicated hydrographic location of the site makes interpretation of the causal factors behind the observed changes difficult to resolve. It is likely that the Russell cycle reflects changes in the NAO index and in the dynamics of the subtropical and subarctic gyres.

Pronounced changes in the plankton of the North Pacific in 1976–77 were contemporaneous with changes in atmospheric pressure and ocean temperature. An intensification and easterly movement of the Aleutian low pressure system occurred with cooler sea surface temperatures in the central and western North Pacific and a warming in Alaska. Changes have also taken place in the ocean circulation in the region. These hydrometeorological events are reflected in the plankton with a doubling of zooplankton biomass in the Gulf of Alaska between the periods 1956–62 and 1980–89. The opposite situation occurred on the west coast of North America where upwelling reduced and colder conditions than usual prevailed. In the subtropical North Pacific vertically integrated chlorophyll levels doubled after the mid-1970s as temperatures decreased and winter winds reduced in intensity. Substantial changes in the zooplankton of the Oyashio and Kuroshio Currents off Japan were also observed. These events were associated with an almost doubling of catches of some salmon species in the Alaskan region and reduced catches further south between Washington and California. The inter-relationship between the responses of planktonic stocks in different regions of the North Pacific is still not clear. There is evidence that a reversal in the regime may have happened in 1989 and that similar events may have occurred in the 1920s and 1940s. The causal factors behind the shifts are still a matter of considerable debate with the possibility that they are a consequence of low frequency–high amplitude climatic cycles, natural step-like changes, stochastic processes, or a combination of these options.

Similar wide-scale and step-wise biotic and environmental changes that occurred in the North Sea circa 1988 have been attributed to a regime shift. While atmospheric variability plays a key role in the overall long-term and regional patterns of plankton, oceanic influences on the North Sea ecosystem have been underestimated in the past. In the North Sea, the exceptional peak in phytoplankton color seen during the late 1980s is associated with an increase in warm-water oceanic inflow entering the North Sea from the shelf edge current. High air temperatures around the British Isles due to the strong westerly wind component in the late 1980s/early 1990s period also occurred. At this time the CPR survey recorded unprecedented numbers of oceanic/Lusitanean plankton species (including doliolids) and the North Sea was characterized by above-average temperatures and salinities. Parallel changes occurred in macrobenthos biomass, and certain species of fish and birds and in levels of oxygen, organophosphate, and nitrate in deep water in the Skagerrak.

Another oceanic incursion took place in the North Sea in 1998 and was associated with the presence of the same plankton species (normally found in more southerly latitudes) seen during the late 1980s and another peak in phytoplankton color. These two peaks in phytoplankton color (late 1980, and 1998) have been linked to an exceptional northward flow in the Shelf Edge Current and throughout the whole of the Rockall Basin. The hydroclimatic mechanisms that convey oceanic water into the North Sea are not well understood. However, the timing of inflow events may be influenced by local wind-driven advection and wider scale oceanic processes in the North Atlantic, which seem to be largely synchronous with the NAO.

The Contribution of Plankton to Climate Change

Plankton Mediation of CO_2 Exchange between the Ocean and Atmosphere

In making up approximately 50% of greenhouse gases in the atmosphere, CO_2 is a key contributor to climate change. Natural sources of CO_2 to the atmosphere are derived almost equally from the oceans (90 $\mathrm{Gt\text{-}C\,y^{-1}}$) and land (100 $\mathrm{Gt\text{-}C\,y^{-1}}$). Concentrations in the atmosphere are in near equilibrium with the surface layer of the ocean – a balance that is achieved through the partial pressure of CO_2 across the surface. Below the surface layer a strong gradient exists to higher CO_2 concentrations in deep, cold, oceanic bottom water. A much smaller proportion of the greenhouse gases methane (CH_4) and nitrous oxide (N_2O) is also sourced from the oceans.

The oceans are central to the global carbon cycle as the major reservoir of carbon and a net sink for excess carbon from the atmosphere. The oceanic reservoir of carbon (excluding sediments) contains approximately 47 times more carbon than the atmosphere and 23 times more than terrestrial biota and soil. Two ‘pumps’ (the biological and solubility pumps) maintain the strong depth gradient to higher CO_2 levels in the deep waters of the ocean. Plankton plays a key role in the biological pump by reducing the concentration of CO_2 at the surface through photosynthetic uptake and as the source of sedimenting particulate organic carbon and later bacterial breakdown to release dissolved inorganic carbon in the deep ocean. Approximately half of the photosynthesis by plants on the earth is carried out by phytoplankton in the sea. The solubility pump is linked to the formation of deep water in polar latitudes, which, because of the higher solubility of

CO_2 in cold water, is rich in CO_2. Without these pumps, levels of CO_2 in the atmosphere would be three times higher than at present, so that any change in their functioning on a global scale could have pronounced implications for CO_2 levels in the atmosphere and hence global warming. A doubling of CO_2 as forecast for the year 2100 would give an enhanced greenhouse forcing of $4\,W\,m^2$. The oceans thus act as an important buffer for CO_2 levels in the atmosphere and through feedback mechanisms could slow down or accelerate the rate of global warming.

Levels of CO_2 in the atmosphere have increased from approximately 280 ppm to 380 ppm in two centuries to the year 2000 and are projected to increase to ~ 750 ppm by 2100. Most of this increase is attributed to anthropogenic inputs, which are still rising and are estimated to average 5.5 ± 0.5 Gt C y^{-1} from fossil fuels and 1.6 ± 1.0 Gt C y^{-1} from changes in tropical land use. Only about half of the anthropogenic inputs are estimated to be retained by the atmosphere (3.3 ± 0.2 Gt C y^{-1}); the oceans (2.0 ± 0.8 Gt C y^{-1}) and the terrestrial biosphere (Northern Hemisphere forests $= 0.5 \pm 0.5$ Gt C y^{-1}) absorb the remainder, leaving the sink for 1.3 ± 1.5 Gt C y^{-1} unaccounted for.

A recent calculation by Takahashi of the annual net uptake flux of CO_2 by the global oceans gives a figure that ranges from 0.60 to 1.34 Gt C y^{-1}. The calculation is still subject to a wide error margin and the range is a consequence of the type of formula used for gas transfer based on wind speed. The temperate and polar oceans of both hemispheres were shown to be the major sinks for atmospheric CO_2 and the equatorial oceans, especially in upwelling regions, were the major sources for CO_2. In these calculations the Atlantic Ocean was singled out as the most important CO_2 sink, providing about 60% of the global ocean uptake, with the Indian and Southern Oceans contributing in equal proportion the remaining 40%. A net balance was achieved in the Pacific Ocean between equatorial sources of CO_2 and sinks in temperate latitudes.

Towards the end of the last glaciation circa 20 000 years ago it is estimated that levels of CO_2 in the atmosphere were approximately 50% lower than the 380 ppm of 2000. In part the lower levels in the Quaternary are likely to reflect increased deep-water formation and a higher flux via the solubility pump to the deep ocean. There is good paleoceanographic evidence that deep-water formation was turned off or on or slowed/accelerated a number of times during the Quaternary. Projected increases in sea surface temperatures in polar latitudes will considerably reduce the solubility of CO_2 in sea water, which together with expected reductions in deep water formation (due to increased stability in surface water from ice melt) is likely to reduce the contribution of the solubility pump to the deep-water CO_2 reservoir. Increased stability in the tropics and temperate latitudes is also likely to reduce upwelling. If these positive feedbacks occur it is likely to lead to a marked reduction in one of the main CO_2 sink routes and an acceleration of the CO_2 rise and global warming.

Changes in the biological pump through increased levels of CO_2 may have an even greater impact. The biological and solubility pumps have opposite seasonal cycles. Photosynthesis is at its maximum in removing CO_2 from sea water during the day time and during summer, the reverse of the pattern seen in the solubility pump. The regional responses on a global scale of these different patterns are still poorly known at the present day, so it is difficult to forecast patterns in the future. Biological responses to global warming are likely on a number of fronts, some of which may already have occurred as described in the first section of this paper.

Dimethylsulfide Production and Marine Phytoplankton

Marine phytoplankton are the primary source of dimethylsulfide (DMS), which is the most abundant volatile sulfur compound in sea water. In terms of potential feedback mechanisms between the plankton and climate, the biogenic production of DMS may have an important role. Although a portion of DMS is oxidized by bacteria and by photochemical reactions within the water column itself, a significant proportion escapes from the sea and is oxidized to sulfur dioxide or to sulfate aerosols in the atmosphere. It is these sulfate aerosols serving as cloud condensation nuclei which may act as a potential feedback mechanism between plankton and climate. Enhanced cloud formation through this mechanism may effect changes in temperature, precipitation light intensity, and light reflectivity (albedo). In the air DMS undergoes photochemical oxidation to sulfate and thus also contributes to the formation of acid rain. The biogenic contribution from the oceans to the global sulfur budget, on an annual basis, is thought to be in the same order of magnitude as anthropogenic fluxes from fossil fuel burning.

While the distribution of DMS is spatially similar to that of chlorophyll *a* (the most widely used measure of phytoplankton biomass) it is believed that phytoplankton species composition is more important than biomass in terms of total DMS production. In polar and coastal regions bloom-forming species of *Phaeocystis* and various dinoflagellates are known to be important contributors to DMS production. It has been suggested that the frequency and intensity of these blooms has been increasing in recent years due to anthropogenic eutrophication; if so the production of DMS may also be increasing. In oceanic regions, massive blooms of coccolithophores (e.g. *Emiliania huxleyi*) have also been correlated with high DMS concentrations.

Iron Fertilization

The cold deep waters of the ocean bottoms are undersaturated in CO_2 and it has been argued that by artifically supplying iron to areas of the ocean that have excess levels of other nutrients, but low levels of chlorophyll, the biological pump could be stimulated, thus reducing atmospheric levels of CO_2. The CO_2 reservoir in the deep ocean would thus be increased. In the equatorial Pacific and Southern Ocean levels of photosynthesis are low and in consequence the nutrients nitrogen, phosphorus, and silicon are in excess. It is believed that the low productivity of these regions is a consequence of an inadequate supply of the trace element iron. Iron is derived from erosion of terrestrial rocks and is transferred to the sea via rivers and in atmospheric dust. Levels in sea water are thus much higher in shelf systems where strong currents through mixing of bottom sediments may provide an additional source. The atmospheric route is the only source for open oceanic waters where concentrations are very low.

It is known from analyses of ice cores that deposition of dust containing iron has varied considerably during the Quaternary and is inversely correlated with levels of CO_2 in the atmosphere during this period. The theory that changes in the supply of iron to oceanic plankton can have a major effect on concentrations of atmospheric CO_2 is known as the 'iron hypothesis'. Based on this hypothesis it has been suggested that by distributing small concentrations of iron over a large area of the Southern Ocean a 'geoengineering' solution may be found to the current rapidly rising levels of CO_2. Mesoscale experiments distributing small quantities of iron in the wake of research ships have been carried out in both the equatorial Pacific and Southern Ocean to test the hypothesis with varying success. It is clear that iron fertilization can stimulate phytoplankton production in these regions. Evidence for this stimulation was seen in the Southern Ocean through enhanced levels of chlorophyll (threefold) evident in satellite imagery as a wave-like ribbon, 150 km long, downstream from the initial experimental site. However, the experiments have not shown any evidence for enhanced sedimentation of the increased production, although associated modeling suggests that sequestration of atmospheric CO_2 by artificial addition of iron to the Southern Ocean is possible.

A counter claim against proponents of the iron hypothesis is that unknown side effects and accelerated production of other greenhouse gases could reinforce rather than ameliorate global warming. The latest experiment led to a large increase in the growth of diatoms and it is clear that any fertilization with iron on a large scale would have considerable effects on the biomass and community structure of the plankton with unknown consequences for oceanic ecosystems and their living resources.

Conclusions

It is clear from recent observations and retrospective analyses of old data sets that pronounced changes have taken place in the ecosystems of the world's oceans in the last 100 years. The extent to which these are natural events as part of short- or longer-term cyclical events, step-like functions, or stochastic processes, or are forced by climate change is still far from clear. What is evident is that major changes in ecosystems can occur with large implications for the productivity, biomass, and composition of all trophic levels as well as the harvesting of living resources. There is some evidence that patterns of change may differ in an opposite sense between different parts of an oceanic basin and that there may be teleconnection links between changes in different oceans. If climate change is forcing these events, they have considerable implications for the CO_2 cycle as positive or negative feedback mechanisms may reinforce or reduce the biological pump. Changes in biodiversity, community and size structure, and production of the plankton are likely to greatly alter the sedimentation to the bottom of the ocean. As a consequence alterations to the community structure may be as important to the CO_2 cycle as gross changes in productivity. Basin-scale changes in circulation that may be forced by climate change are likely to have a profound effect on the productivity of the plankton; these may be reflected in the direction and strength of major currents, the degree of mesoscale mixing, eddy formation and upwelling, and the intensity and slope of the thermocline. Such physical changes will also influence the contribution of the solubility pump.

Understanding of the link between climate and plankton is still at an early stage, largely because of a lack of field information. Many parts of the world's ocean are little studied and there is no systematic system to collect time-series information to relate to the much better data being produced by national meteorological surveys. Because plankton integrates a wide range of environmental signals it may provide an early warning of environmental change. Evidence from the Pacific indicates that regime shifts, for example, can be identified earlier using plankton than from considering climate data alone. To advance our understanding international programs such as the Global Ocean Ecosystem Dynamics (GLOBEC) project are evaluating the relationship between plankton and climate. The Global Ocean Observing Scheme (GOOS) is developing a global operational monitoring program for the oceans that includes a biological component.

See also

Air–Sea Gas Exchange. Air–Sea Transfer: Dimethyl Sulphide, COS, CS_2, NH_4, Non-methane Hydrocarbons, Organo-halogens; N_2O, NO, CH_4, CO . Bottom Water Formation. Carbon Cycle. Carbon Dioxide (CO_2) Cycle. Continuous Plankton Recorders. Ekman Transport and Pumping. El Niño Southern Oscillation (ENSO). El Niño Southern Oscillation (ENSO) Models. Exotic Species, Introduction of. Fisheries and Climate. Heat and Momentum Fluxes at the Sea Surface. Holocene Climate Variability. Iron Fertilization. Marine Snow. North Atlantic Oscillation (NAO). Ocean Carbon System, Modelling of. Paleoceanography, Climate Models in. Phytoplankton Blooms. Plankton. Primary Production Distribution. Protozoa, Planktonic Forminifera. Redfield Ratio. Thermohaline Circulation.

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PLANKTON VIRUSES

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Introduction

Although they are the tiniest biological entities in the sea, typically 20–200 nm in diameter, viruses are integral components of marine planktonic systems. They are extremely abundant in the water column, typically 10^{10} per liter in the euphotic zone, and they play several roles in system function: (1) they are important agents in the mortality of prokaryotes and eukaryotes; (2) they act as catalysts of nutrient regeneration and recycling, through this mortality of host organisms; (3) because of their host specificity and density dependence, they tend to selectively attack the most abundant potential hosts,