

4. LIFE SUSPENDED IN WATER: THE PLANKTON

Geoff A. Boxshall

The Natural History Museum, London, UK



4.1. INTRODUCTION

THE EARTH IS A WATERY PLANET, with 71% of its surface covered by oceans. A more appropriate name would have been the Blue Planet. The pelagic zone of the open ocean, away from the seabed and away from the coastline, is the largest habitat on the planet, comprising approximately 1347 million km³. This enormous volume is inhabited by a diverse community of micro-organisms and metazoan animals – the plankton. The word plankton is derived from the Greek word for wandering and is used to describe the community of organisms that is transported around by the motions of the ocean currents and water masses. Planktonic animals can swim, but because they typically have a small body size, they cannot swim fast enough or far enough to move independently of the water mass within which they are found. There are planktonic species with large body size, including colonial salps of the genus *Pyrosoma* which may attain lengths in excess of 4 metres in tropical waters, and medusae such as the recently discovered big red jellyfish, *Tiburonia granrojo*, but these are exceptions and even with their large bodies they are not capable of independent motion against the flow of the water masses.

The pelagic water column is inhabited by a diverse and dynamic community comprising both holoplanktonic organisms, that spend their entire life in the plankton, and meroplanktonic organisms that are planktonic for only part of their lives. The meroplankton is dominated by larval forms and its composition varies strongly with the season, especially in temperate latitudes. Meroplanktonic larvae eventually mature and either become nektonic (capable of swimming against the flow of the water mass), for example fish larvae, or benthic (living on the sea floor), for example echinoderm or bivalve mollusc larvae. Planktonic organisms are patchily distributed in space and in time. This characteristic makes the study of plankton dynamics problematic: detecting change through time requires rigorous statistical analysis capable of picking

◀ **Photo 4.1: Blue whale (*Balaenoptera musculus*).** This cetacean, the largest animal to ever inhabit the seas, feeds exclusively on plankton, particularly krill.



Photo 4.2: Antarctic krill (*Euphausia superba*). These small planktonic crustaceans form the base of the food chain in Antarctic ecosystems.

out trends against a background of variability due to horizontal or vertical patchiness.

Planktonic systems are largely driven by the capture of solar energy by photosynthesis, which is confined to the well-lit surface waters where light levels are adequate. Primary production, both by eukaryotic algae and by photosynthetic bacteria, can also be dependent on nutrient levels, the low availability of which may limit primary production even in well-lit waters. Ocean circulation patterns, stratification of the water column, and upwelling events can all have a profound effect. Plankton is found at the greatest abundance in near-surface waters but occurs throughout the water column, down to the deepest ocean trenches. Below the depth where net primary production ceases, planktonic organisms utilise marine snow – organic material sinking out from the upper horizons of the water column. The flux of sinking material is seasonal in temperate zones and a discrete seasonal pulse of material has been detected entering the abyssal zone after the spring bloom in the northern hemisphere. So changes at the surface can affect processes in deep water on relatively short time scales.

4.2. KEY CHALLENGES

The scientific and technical challenges facing researchers working on the plankton are essentially the same as those facing marine biology as a whole. The three key challenges are:

- Discovery: to search for unknown life forms and survey new habitats to identify areas of particular importance
- Understanding: to make observations and undertake experiments at all temporal and spatial scales
- Prediction: to develop models to allow us to predict future changes in marine systems in response to environmental change, whether natural or anthropogenic.

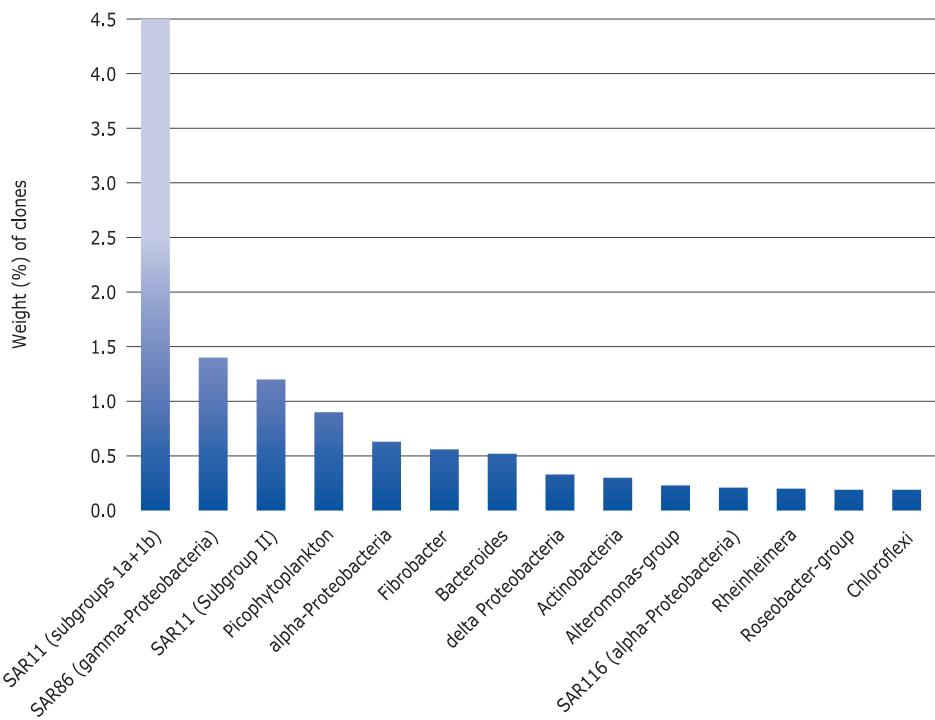
Running across all these challenges are issues of scale, in particular the need to integrate data from the ultra-small scale of molecular biology up to global scales using remote sensing data from Earth observation satellites. In addition we need to be able to generalise across scales, working from observations on individuals or local populations up to ocean basin or global scale processes.

4.2.1. Discovery

In 2004 Craig Venter and colleagues, using shotgun sequencing, examined the genes present in samples of water from the Sargasso Sea, finding 1,214,207 new genes and approximately 1,800 new species of microbial organisms (figure 4.1). The scale of these discoveries indicates that up to 99% of the diversity of life in the oceans may still remain to be discovered, and that most of it is microbial!

Such discoveries of new marine micro-organisms are not restricted to near-surface waters. Green sulphur bacteria are anaerobes (organisms that grow and reproduce in the absence of molecular oxygen) that require light for growth by the oxidation of sulphur compounds to reduce CO_2 to organic carbon, but they are capable of photosynthetic growth at extremely low light intensities. New kinds of green sulphur bacterial species have just been described from a deep-sea hydrothermal vent, where the only source of light is geothermal radiation that includes wavelengths absorbed by photosynthetic pigments of this organism.

Smaller still than the bacteria are marine viruses. Viruses are extremely abundant in the plankton and have been estimated to be the second largest

Figure 4.1. Bacterial diversity in the Sargasso Sea

Source: Venter et al., 2004.

component of oceanic biomass after the bacteria. In coastal waters, there may be about 10^7 viruses in one millilitre of seawater, but this abundance decreases both with increasing depth and distance from the shore. Not only are marine viruses abundant but they also exhibit immense genetic and biological diversity.

It is not just the marine microbial organisms that are poorly known. It is estimated that there are also thousands of new animal species awaiting discovery, and many other recognised species where the application of novel methods of study is refining our concept of species boundaries. For example, it is now becoming apparent that some of the so-called cosmopolitan species of marine zooplankton are in fact complexes of closely related species, each predominant in a particular ocean basin. Molecular methods have revealed these problems, but careful morphological study can also help to solve them.

The plankton in deeper oceanic waters has been relatively poorly studied: the oceans are vast and few vessels are equipped to sample in midwater at depths

in excess of 2,000 metres. The abundance of the zooplankton decreases with increasing depth, but rises again in the near-bottom waters. This depth zone at the base of the water column, referred to as the hyperbenthic, is a region of dynamic interaction between the water column and the sea bed, but it is difficult to sample. Nets must be towed very close to the bottom (ideally only 1 metre above the sediment), without colliding with it. Successful sampling in the hyperbenthic has demonstrated that it is home to numerous new species: for example, of copepods; diminutive crustaceans (relatives of crabs and shrimps), which typically have a body length of only 1 to 2 mm. The hyperbenthic is a rich source of new species, new genera and even new families of copepods, but obtaining good samples remains one of the most serious sampling challenges in deep-sea biology.

Much larger zooplanktonic species are still being discovered. Off the coast of California, a blood-red jellyfish, *Tiburonia granrojo* (photo 4.3), has been observed several times in Monterey Submarine Canyon at depths of 645 metres and more. Thus far only a single specimen has been caught, but these predators range in size between 60 and 90 cm in diameter. An unusual feature of this new species is that it lacks tentacles around the margin of its bell-shaped body,



Photo 4.3: *Tiburonia granrojo*. The “Big Red” jellyfish, which grows up to 90 cm, was recently discovered off the eastern Pacific coast of the United States.

which are used to catch prey in most jellyfish. Instead it has between four and seven thick wrinkled arms on its under surface.

Using an astonishing range of techniques, from DNA extraction of water samples to nets on the robotic arms of manned submersibles, marine biologists continue to find remarkable new forms of life. These may range in size from the smallest microbial organisms with body sizes measured in microns, to large animals measuring nearly a metre in length. It is safe to assume that many novelties await discovery in the vastness of the pelagic realm.

4.2.1.1. HOTSPOTS

The concept of biodiversity hotspots as areas of exceptional biotic richness set against a background of relatively low diversity has been widely adopted as a method of identifying priority areas for conservation programmes. Relatively few such hotspots have been identified for the marine realm, apart from coral reefs and the hydrothermal vents and cold seeps that are described in chapter 3. In part, the difficulty in applying the hotspot concept to the plankton reflects the lack of obvious physical barriers in the oceans. However, recent research has shown that the plankton of flooded marine and anchialine caves is remarkably rich in novel animal species.

Anchialine habitats are flooded coastal caves and groundwater habitats that lack any direct surface connection with the open sea. They are inhabited by remarkably specialised animals, many of them representing long-term survivors of ancient lineages, which are now threatened by changes in their fragile habitat. In the past 25 years, over 250 new species, at least 17 new families and even a new class of shrimp-like crustaceans – the Remipedia – have been described from the plankton in anchialine caves (photo 4.4), particularly on tropical and subtropical islands.

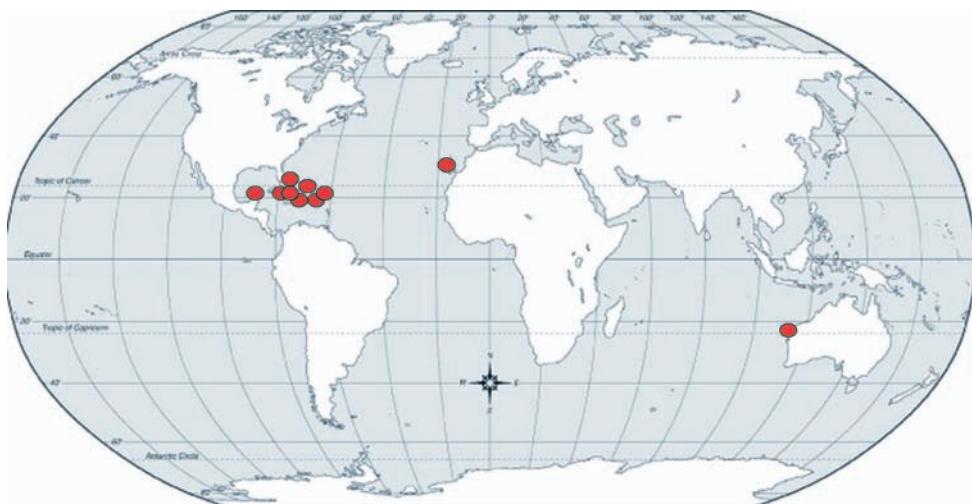
This extraordinary degree of novelty qualifies anchialine habitats as uniquely important. An extremely high proportion of the crustaceans inhabiting these caves can be regarded as living fossils. Studies on such primitive animals have shed new light on the evolutionary history and relationships of many groups of animals. The animals living in the caves also have unusual genetic properties, such as the ability to survive in water with very low levels of dissolved oxygen. The powerful techniques of modern genetics mean that uniquely adapted animals such as these are a potential source of genes.



Photo 4.4: Remipede from anchialine cave on the Exumas Cays, Bahamas. There are only 16 species of remipedes known worldwide and all occur only in anchialine caves.

The exploration of caves is still in its infancy, and there are significant gaps in our knowledge and in our understanding of how the caves were colonised and where the colonists originated. For example, the known distribution pattern of remipedes is remarkable: fourteen of the sixteen species occur on Caribbean islands and the Yucatan peninsula (map 4.1). Two other species are known: one

Map 4.1: Known distribution of remipede species



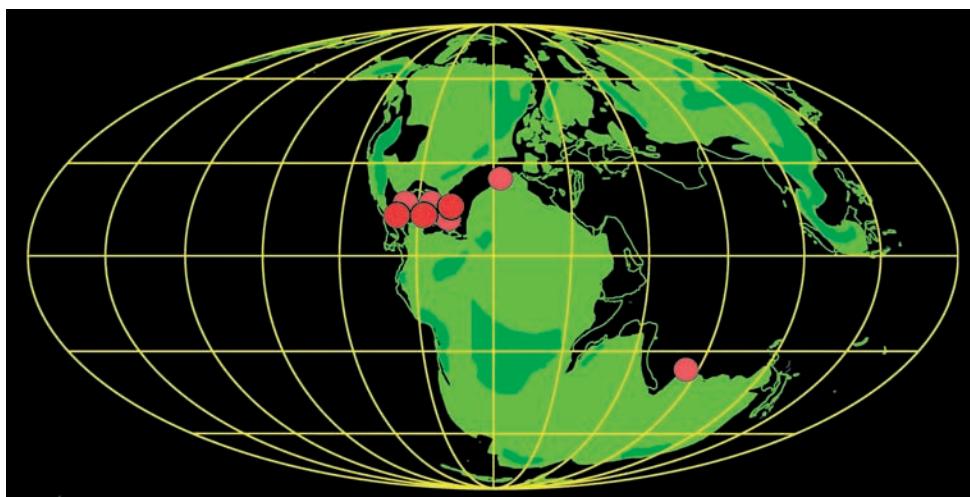
from a flooded lava tube in Lanzarote in the Canary Islands, the other from a cave in Western Australia. Other crustacean components of the anchialine faunal suite, such as thaumatomcyprid ostracods, epacteriscid and speleophriiid copepods, each display very similar patterns. How can we explain such extremely disjunct distribution patterns?

The emerging hypothesis to account for the remarkable distribution of remipedes and other members of the fauna implicates tectonic plate movements over geological time periods (map 4.2).

The suggestion is that the anchialine fauna was widely distributed around warm, shallow margins of the ancient Tethys Sea. Elements of the fauna then colonised caves from adjacent shallow water and were subsequently separated when tectonic plate motions resulted in the opening of the Atlantic Ocean and the eventual closure of the Tethys Sea. The fauna must have persisted in cave systems at these sites through geological time scales and through major changes in global sea-level, and it is likely that the cave systems served as thermal refuges for relict fauna during the last Ice Age, for example. These ideas can be tested relatively simply using molecular methods, but this has not been possible to date because of the difficulty in sampling many of the caves.

It is imperative that we locate and explore new anchialine sites around the world and describe their inhabitants before it is too late. This research will help us to answer topical ecological and evolutionary questions, such as, where did these

Map 4.2: A reconstruction showing the distribution of remipede sites relative to the positions of landmasses 120 million years ago, during the Jurassic period



uniquely primitive cave faunas originate, and how were their amazing distribution patterns generated. We must also undertake a threat assessment for the most important major anchialine sites, and then promote the inclusion of anchialine habitats in coastal management to policy makers and conservationists.

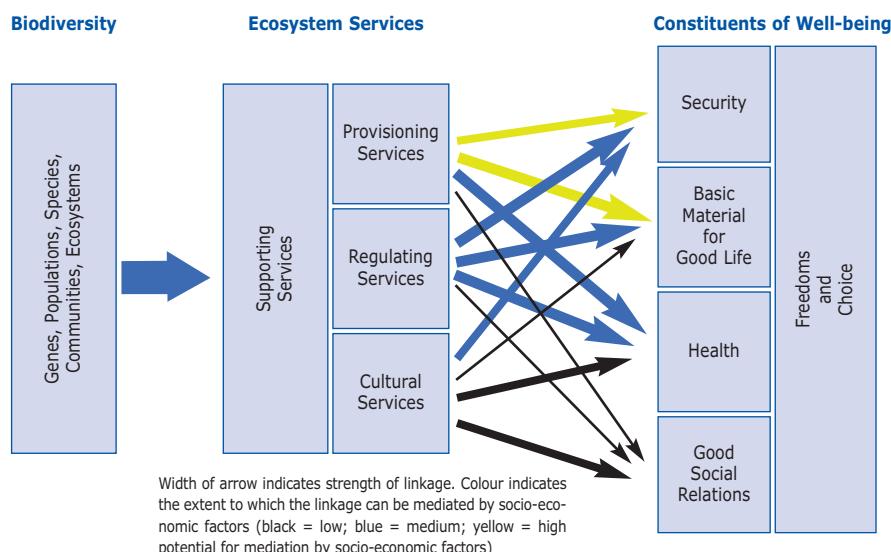
The discovery of new species and new distribution patterns contributes to the development of knowledge on oceanic systems. It allows us to build the baseline assessment of what occurs where in the oceans. This baseline assessment is an essential initial step, since it will provide the benchmark against which changes can be monitored and measured.

4.2.2. Understanding

Our improved understanding of ecology and of global-scale cycles in all kinds of elements and resources has resulted in a conceptual change in how we view the Earth's ecosystems. In part, this change has emerged from a novel way of quantifying the dependence of humankind on the provision of services and functions by the world's natural ecosystems (Costanza et al. 1997; figure 4.2).

Ecosystem services have been categorised into provisioning services, such as the provision of food for human consumption, regulating services such as the

Figure 4.2: Linkages among biodiversity, ecosystem services, and human well-being



Source: *Millennium Ecosystem Assessment*, Washington, DC, World Resources Institute, 2005.



Photo 4.5: Larvae of *Semibalanus balanoides*. Many bottom-living organisms have larval stages that are temporary members of the plankton community, such as these naupliar larvae of acorn barnacles.

role of the ocean in climate regulation (the transport of heat northwards in the Atlantic by the Gulf Stream), cultural services, such as ecotourism activities like viewing whales, and supporting services, such as gas regulation in the atmosphere. The oceans in general and the vast pelagic-planktonic system are pivotal in the provision of many of these ecosystem services and functions upon which continued human well-being depends.

Mankind has generally taken such ecosystem services for granted, but recent improvements in our understanding of Earth Systems have strongly emphasised our dependence upon natural systems for the oxygen we breathe, the food we eat and the water we drink. All living organisms and the biosphere they inhabit interact as components of a vast global system, and the dynamics of this system are studied in terms of how matter flows through them – as global biogeochemical cycles.

4.2.2.1. THE CARBON CYCLE AND PHOTOSYNTHESIS

Oceans play an integral part in the natural processes of cycling carbon on a global scale – the carbon cycle. Over the past 200 years, since pre-industrial

times, it is estimated that the oceans have absorbed about half of the CO₂ emissions produced by burning fossil fuels and cement manufacture. The oceans and the organisms they support contain an estimated 38,000 gigatonnes of carbon, which account for about 95% of all the carbon that is in the oceans, atmosphere and terrestrial system combined. So, the oceans contain an enormous reservoir of carbon, but their capacity to absorb CO₂ from the atmosphere will reduce as the level of atmospheric CO₂ rises.

The abundance of life on Earth is almost entirely supported by biological photosynthesis, which uses light energy to fix CO₂. The primary source of light in natural habitats is the sun, so photosynthesis is largely, but not exclusively, restricted to solar photic environments on the surface of the Earth. The marine eukaryotic phytoplankton, especially the diatoms and to a lesser extent the dinoflagellates, were long considered the dominant photosynthetic organisms in the oceans. However it has recently been discovered that bacterial photosynthesis occurs on a large scale in the oceans. Craig Venter et al. (2004), for example, found a total of 782 Rhodopsin-like genes in the Sargasso Sea. Rhodopsin-mediated photosynthetic production by bacterial plankton may have significant effect on energy and carbon fluxes in the oceans.

The role of marine plankton in global biogeochemical cycles is becoming more widely understood (Raven and Falkowski 1999). The photosynthetic activity of the bacterioplankton and phytoplankton serves to fix carbon, which is then available to other consumer organisms in the plankton. Size is important here – as a determinant of whether the primary production flows into the microbial foodweb, or the traditional food web in which the larger phytoplankton are consumed by zooplankton which are, in turn, consumed by fish.

Microbial foodwebs are based on photosynthetic organisms, the so-called picoplankton, that are so small that most of the organic matter produced cannot be used by zooplanktonic herbivores such as the copepods. This matter is transferred through bacteria, small heterotrophic flagellates and ciliates. This kind of food web appears to be the most common in the oceans, especially in stratified and oligotrophic (low productivity) regions, where it is responsible for driving most of the transfer of energy and matter in the epipelagic zone. The tight coupling between consumers and producers is a characteristic feature of microbial food webs, resulting in a dominance of processes that recirculate energy, rather than processes that export energy and matter from the system. These two kinds of foodwebs coexist and are interconnected. Small zooplanktonic copepods are of potential importance in linking these foodwebs. Firstly, their small body size suggests that they are able to graze on smaller organisms, such as the smallest

nanoplanktonic fraction, thereby bypassing several trophic levels. Secondly, in contrast to medium and large-sized copepods, which produce large faecal pellets that can sink out of the photic zone and thus export carbon out of the surface waters, small copepods produce small faecal pellets. These have low sinking rates, and are probably consumed before sinking out of the euphotic zone. Finally, some copepods, such as species of the genus *Oncaea*, graze on marine snow and others, such as species of *Oithona*, feed on the faecal pellets of other zooplankters. In effect this enhances the recycling processes in the upper water layers and retards the vertical export of matter and energy.

The movement of carbon from the surface to the depths is known as the biological pump – the sum of the biologically-mediated processes that transport carbon from the well-lit euphotic zone to the interior of the ocean. The scale of the biological pump contributes to the oceans being the largest active pool of carbon on the planet. There is also an inorganic component to the flux of carbon exported to deep ocean waters, in the form of calcium carbonate shells or plates produced by planktonic organisms such as coccolithophores (photo 4.6) and foraminiferans.

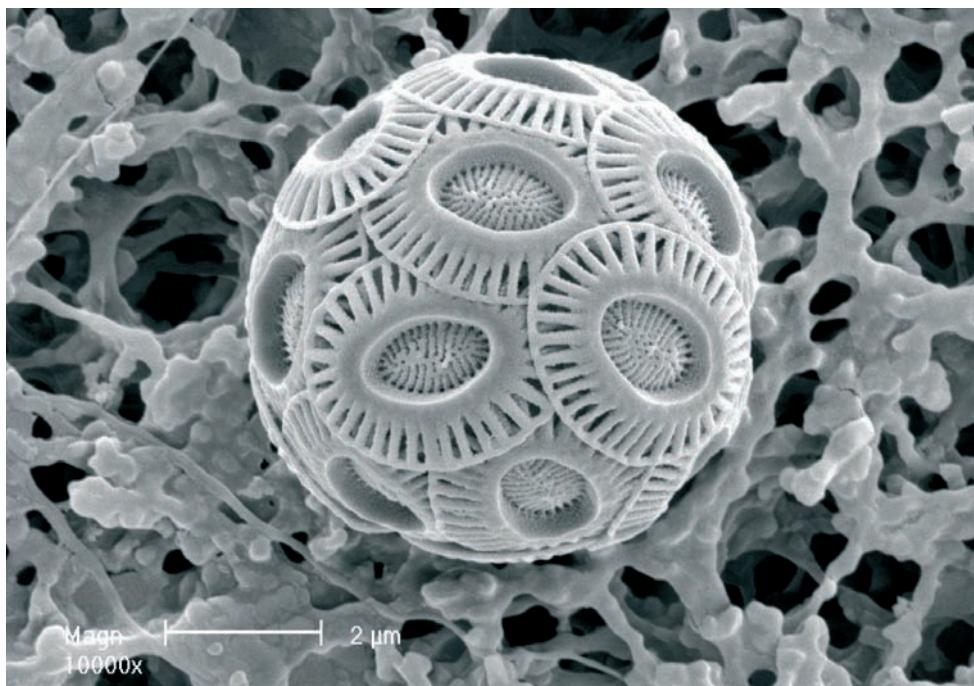


Photo 4.6: Coccolithophore *Emiliania huxleyi* through the microscope. This scanning electron micrograph shows the array of complex calcium carbonate plates (liths) covering the alga's outer surface.



Photo 4.7: Satellite image showing extensive blooms of coccolithophore algae off the coast of France and the UK

Under certain conditions coccolithophore algal blooms occur (photo 4.7) and large quantities of inorganic calcium carbonate (in the form of liths) are produced. The calcium carbonate dissolves at a rate dependent upon local carbonate chemistry, involving factors such as temperature and depth. However, these dissolution processes are generally slower than synthesis. Overall the biological pump transports material from the ocean surface to deeper waters.

4.2.2.2. THE NITROGEN CYCLE

The oceans are also pivotal in the global nitrogen cycle. It has long been known that the oceans contain nitrogen-fixing cyanobacteria, and the filamentous *Trichodesmium* (photo 4.8) was assumed to be the predominant organism responsible in the oceans. However, the abundance of *Trichodesmium* was unable to account for the rates of fixation observed. Recent studies (Zehr et al. 2001) have found evidence of abundant unicellular cyanobacteria in the size range 3 to 10 μm , which express nitrogenase enzymes – an indication of their nitrogen-fixing ability. These picoplanktonic organisms have not yet been

Photo 4.8: Colony of *Trichodesmium* filaments, a large photosynthetic and nitrogen-fixing cyanobacterium



fully studied but these results seem to indicate the existence of a different pathway in the foodweb from other nitrogen-fixers.

The opposite function – the conversion of nutrients into nitrogen gas – is performed by other picoplanktonic bacteria. Recent work has revealed that much of this reverse conversion is not carried out by denitrifying bacteria converting nitrate to nitrogen gas in the absence of oxygen, as formerly believed, but by anammox bacteria (photo 4.9) that directly remove ammonium from the ocean (Kuypers et al. 2005).

These bacteria, discovered first in the oxygen poor waters of the Black Sea, have now been found in the open ocean, in oxygen-poor areas of the South Atlantic where upwelling occurs off the coast of Namibia, and it has been calculated that 30% to 50% of the global conversion of nutrients to nitrogen gas occurs in these areas. This discovery has major consequences for our understanding of the global nitrogen cycle. And, in this complex interconnected Earth system, this change in the global nitrogen budget has knock-on effects for the global carbon cycle.

Due to its large colony size, *Trichodesmium* is the most conspicuous of the marine nitrogen-fixing organisms. Its colonies manage to thrive in the nutrient-poor, open ocean, pelagic environments in which levels of the essential element phosphorus are extremely low. One factor in its success is the recently

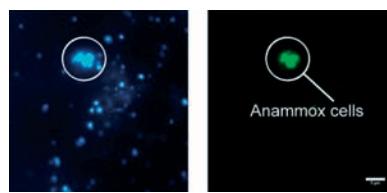


Photo 4.9: Flourescent micrographs showing Anammox bacteria. The term *Anammox* refers to the process of anaerobic ammonium oxidation.

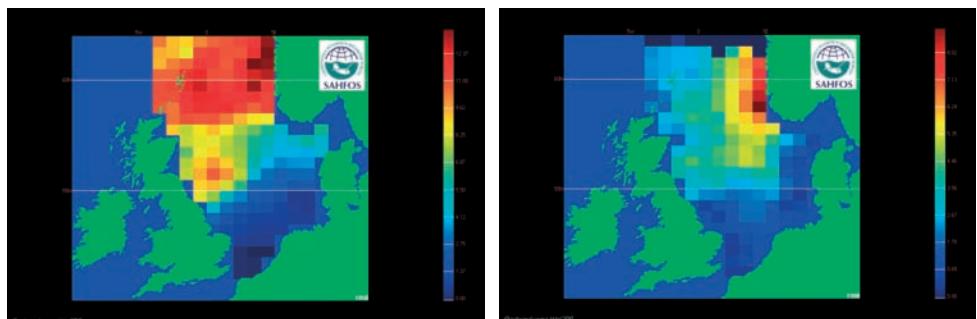
discovered ability to exploit phosphonates, previously thought to be unavailable to phytoplankton, as a source of phosphorus. In doing so, *Trichodesmium* increases the bioavailability of phosphorus to other planktonic organisms in both the microbial and traditional foodwebs. With its dual role in both the carbon and nitrogen cycles, *Trichodesmium* has become a model system for the study of plankton physiology: these new discoveries indicate that detailed study of the diversity of microbial primary producers will reveal a similar diversity in basic physiological processes.

Marine viruses are a significant cause of planktonic microbial mortality and, as such, also play a role in marine nutrient cycles. Viruses act as catalysts accelerating the transformation of nutrients from a particulate state (i.e., living micro-organisms) to a dissolved state, from where they can be readily incorporated back into the microbial community. This so-called viral shunt has the effect of decreasing the efficiency of the transfer of carbon to higher trophic levels, of increasing community respiration and, indirectly, of reducing the export of carbon from the euphotic zone into deeper waters. Even the smallest of micro-organisms can thus have a significant impact on global biogeochemical cycles.

4.2.2.3. DRIVERS OF CHANGE: DETECTING AND MONITORING CHANGE

There is considerable concern over potential changes in marine biodiversity and ecosystem functioning in response to global climate change. Planktonic organisms are particularly useful as ecological indicators, and detailed study of patterns of variation in plankton can help us distinguish between natural variability and anthropogenic change. Using long time series data from the Continuous Plankton Recorder survey, it has been possible to demonstrate shifting biogeographical patterns in the North Atlantic. It is apparent that several sub-tropical plankton species are shifting their distributions northwards in response to global warming; at the same time some northern species, such as the abundant copepod *Calanus finmarchicus*, are retreating pole-wards from more southerly locations (map 4.3). Recent research (Beaugrand et al. 2002) has shown a 10° latitudinal northward shift for warm-water copepods, with a corresponding retreat of cold-water species.

Long-term data sets for marine organisms are rare. The CPR survey has been undertaken, with minor interruptions, for over 70 years and is the longest running and most comprehensive series anywhere in the world. Research funding agencies often fail to recognise the immense value of time series data and many

Map 4.3: Gridded distribution of *Calanus finmarchicus* in the North Sea

Comparison of 1958 (left) and 1988 (right) distributions showing the northerly retreat of this cold-water copepod.

Source: Vezzulli et al., 2005.

series are under threat – despite the unique perspective they provide on environmental change issues. One of the practical challenges for marine biologists is to secure the future of such surveys.

Another fascinating finding that has emerged from long time series CPR data is the disruption of the planktonic foodweb resulting directly from global warming during the latter half of the 20th century. The traditional foodweb begins with phytoplanktonic diatoms which are consumed by copepods, which are extremely efficient at catching algal cells. The copepods are then eaten by secondary consumers in the food chain, including most larval fishes, such as cod, and some adult fishes, such as herring. In the temperate North Atlantic during winter, diatoms are relatively inactive: light levels are low so photosynthesis rates are low. In the spring, light levels increase, the levels of nutrients such as phosphates and nitrates are high since the water column is well mixed by winter storms, and the diatoms begin to bloom. The spring algal bloom provides an enormous resource, a massive input of biomass and energy into the planktonic system. The spring algal bloom is closely followed by a peak in zooplankton abundance. The zooplanktonic copepods reproduce rapidly, exploiting the available algal biomass. Fish larvae then feed on the larger and longer lived copepods. Recent research (Edwards and Richardson 2004) has shown that the timing of the spring algal bloom is governed by day-length, and has not changed significantly in response to global warming. In direct contrast, the timing of peak zooplankton abundance responds to temperature, and has gradually been occurring earlier in the year as ocean temperatures have risen. There is a temporal mismatch in the system and the zooplankton are now reproducing



Photo 4.10: Tunid fisheries. Tunids are a high value marine resource, but the lack of regulation of fisheries in international waters has dramatically reduced catches: marine protected areas on the high seas are urgently needed.

too early, slightly in advance of the algal bloom – their food supply. The organisms making up this system have co-evolved over millions of years but the system is now under stress.

Living organisms are highly adaptable but the rate of change due to global warming is unprecedented. The planktonic system is failing to adapt. The lack of available copepods as food for larval fishes will have consequences for recruitment to fish stocks and, indeed, this mismatch between trophic levels and functional groups has already been implicated as a factor in the failure of the North Sea cod stock to recover despite efforts to control fishing intensity (Beaugrand et al. 2003). The plankton ecosystem will not entirely collapse as a result of such changes. The spring algal bloom will remain a massive resource and organisms will move in to exploit it – but these organisms may be integral components of the microbial foodweb, or they may be unsuitable as food for fish larvae. The danger is that the planktonic system may have irreversibly changed. We can predict with reasonable certainty that the system will not behave as it has done for recent centuries, and this will have pro-

found implications for the fishing industry. Such predictions tend to be applicable only to a single system in a particular region, and we need to progress to larger scale and more rigorous predictions. In order to achieve this, it will be necessary to develop new time series that provide a network of sampling points around the world and allow us to build a more coherent picture of the state of the oceans.

Another driver of change, even in marine planktonic systems, is invasive species. Non-indigenous gelatinous zooplankton species have been introduced in various regions, and have been implicated in major changes to semi-enclosed ecosystems. For example, the predatory ctenophore *Mnemiopsis leidyi* was introduced into the Black Sea in the early 1980s, probably in ship ballast water. A massive increase in its abundance was followed by sharp declines in mesozooplankton and in ichthyoplankton (eggs and larvae of sprat and anchovy) (Kidneys 2002). Interestingly the explosive increase in *Mnemiopsis* was preceded by a reduction in the numbers of plankton-feeding fishes by overfishing. The reductions in these fishes, which are the main competitors for *Mnemiopsis*, could be a possible reason for the outbreak, demonstrating again the vulnerability of stressed systems.

Blooms of gelatinous zooplankton have become increasingly common, and deleterious effects have been reported on ecosystems and fisheries in eastern Mediterranean waters, off Japan and in the North Sea. Similarly, the increase in jellyfish biomass in the Bering Sea, dominated by *Chrysaora melanaster*, is predicted to have effects on groundwater fisheries. Species dominance patterns may change in time but sudden changes, such as jellyfish blooms and invasions, are likely indications of ecosystem instability. In addition, our emerging understanding of the role of rare species in ecosystems indicates that their weak trophic links may serve to enhance the stability of the entire food-web. An important challenge is to develop the theoretical basis of the relationship between stability and species diversity in marine planktonic systems. Existing theory, developed using terrestrial model systems, does not translate well into the marine environment, and we need to better understand why some marine systems are more vulnerable to invasion than others and why rare species can suddenly become common.

4.2.3. Prediction

As well as continuing to document and describe the living components of the global ocean, and as well as continuing to improve our understanding of their

interactions and their role in the global biogeochemical cycles, we need to use the products of this research effectively. In particular, we need to make long-term observations and measurements, and to incorporate them into developing models which will allow us to predict how abiotic factors such as global warming, sea-level rise, and acidification (due to rising CO₂) might cause changes in the plankton. It is already possible to obtain satellite data on a global scale for factors such as sea surface temperature (map 4.4), surface chlorophyll, and carbon export. The integration of these global measures with more regional and local biological data is an important area of active research.

The development of large-scale predictive models of climate change has been an enormous asset to the world community of climatologists. The International Panel on Climate Change increasingly relies on complex models, run on supercomputers, for prediction of the effects of global warming on regional climates for decades to come. These models have enabled them to effectively communicate ideas on the behaviour of complex systems to the public and to policy makers, and even to communicate the levels of uncertainty associated with the predictions. In the arena of biological oceanography, the biggest challenge we face is to develop complex models that will enable us to make robust predictions about how the planktonic system will change, and whether the oceans will continue to provide the ecosystem services upon which continued human well-being depends.

Map 4.4: Global sea surface temperature. On a rising scale from violet (approximately 0°C) to red (approximately 28°C).

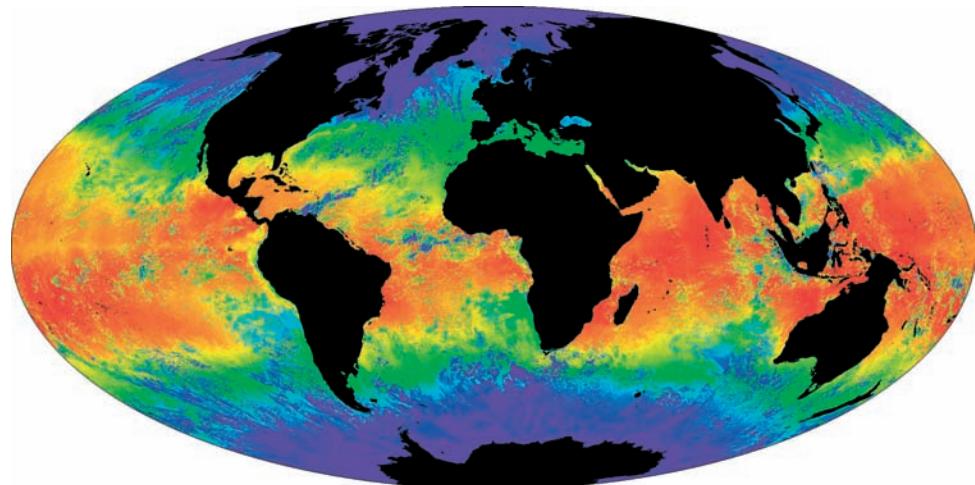




Photo 4.11: Jellyfish (*Cotylorhiza tuberculata*). In open pelagic waters, large gelatinous plankton like this jellyfish provide shelter and a focal point for the behaviour of small fishes.

4.3. SUMMARY

It is remarkable how poorly we understand the biology of the oceans that surround us. In view of their vastness, perhaps it is not surprising that our knowledge of the microbes that inhabit the oceans is fragmentary, but the development of new molecular methods of study has provided powerful tools that are already beginning to reshape our ideas. Microbial life in the oceans is far more diverse than hitherto realised, and the diversity of microbial physiology is changing established concepts of the processes by which material flows through the global biogeochemical cycles. In functional terms, it has become clear that the microbial foodweb is of at least equal importance to the traditional diatom-copepod-fish dominated foodweb. The final goal of marine biological research must be to develop models that will encapsulate our knowledge of the planktonic biodiversity and our improving understanding of how planktonic systems function. These models will allow us not only to predict change but, more importantly, to use our knowledge in sustainably managing and using the oceans for the benefit of mankind long into the future. The scientific challenges we face in getting to that position are:

- To document and describe the diversity of life, including microbial life, in the plankton
- To explore and study unique biodiversity hotspots, such as flooded marine caves
- To understand the functional role of biodiversity in global cycles
- To measure how biodiversity is changing over time and to develop a global network of observation sites
- To identify the drivers of change in the plankton
- To develop robust models of how the planktonic system will change in response to environmental change at regional and global levels.

REFERENCES

BEAUGRAND G., K. M. BRANDER, J. A. LINDLEY, S. SOUSSI, and C. P. REID. “Plankton effect on cod recruitment in the North Sea”. *Nature* 426 (2003): 661-664.

BEAUGRAND, G., C. P. REID, F. IBÁÑEZ, J. A. LINDLEY, and M. EDWARDS. “Reorganization of North Atlantic marine copepod biodiversity and climate”. *Science* 296 (2002): 1692-1694.

COSTANZA, R., R. D’ARGE, R. DE GROOT, S. FARBER, M. GRASSO, B. HANNON, K. LIMBURG, et al. “The value of the world’s ecosystem services and natural capital”. *Nature* 387 (1998): 253-260.

EDWARDS, M., and A. J. RICHARDSON. “Impact of climate change on marine pelagic phenology and trophic mismatch”. *Nature* 430 (2004): 81-83.

KIDNEYS, A. E. “Rise and fall of the Black Sea ecosystem”. *Science* 297 (2002): 1482-1484.

KUYPERS, M. M. M., G. LAVIK, D. WÖBKEN, M. SCHMID, B. M. FUCHS, R. AMANN, B. BARKER JØRGENSEN, and M. S. M. JETTEN. “Massive nitrogen loss from the Benguela upwelling system through anaerobic ammonium oxidation”. *PNAS* 102 (2005): 6478-6483.

RAVEN, J. A., and P. G. FALKOWSKI. “Oceanic sinks for atmospheric CO₂”. *Plant Cell Environ.* 22 (1999): 741-755.

VENTER, J. C., K. REMINGTON, J. F. HEIDELBERG, A. L. HALPERN, D. RUSCH, J. A. EISEN, D. WU, et al. “Environmental genome shotgun sequencing of the Sargasso Sea”. *Science* 304 (2004): 66-74.

VEZZULLI, L., P. S. DOWLAND, P. C. REID, N. CLARKE, and M. PAPADAKI. *Gridded database browser of North Sea plankton: fifty years (1948-1997) of monthly plankton abundance from the Continuous Plankton Recorder (CPR) survey [CD-ROM]*. Plymouth (UK): Sir Alister Hardy Foundation, 2005.