chloride. This implies that weathering influences the concentrations of the major ions in the runoff from the continents.

Minor Constituents

Some minor constituents show a conservative type of distribution in the oceans. They are the alkali ions Li^+, Rb^+, and Cs^+, besides $MoO_4{}^{2-}$ and Tl^+. Obviously, the organisms only use small amounts of molybdenum. However, in waters with anoxic basins (some fiords and the Black Sea), molybdate is depleted. In addition, $WO_4{}^{2-}$, $ReO_4{}^{2-}$, and U(VI) show conservative-type oceanic distributions.

Conclusions

The major constituents of sea water are present in practically constant proportions. The main ions include the alkali ions Na^+ and K^+ and the alkaline earth ions Mg^{2+} and Ca^{2+}, in addition to chloride (Cl^-) and sulfate ($SO_4{}^{2-}$). Their concentrations are also proportional to the salinity. In spite of the weathering and recycling processes and the hydrothermal reactions with hot basalt in rift zones there are only slight perturbations of the steady state. Deviations from a conservative behavior may be detected by accurate analytical methods and studies of ancient marine waters.

See also

Breaking Waves and Near-surface Turbulence. Calcium Carbonates. Carbon Cycle. Copepods. Dispersion from Hydrothermal Vents. Freshwater Transport and Climate. Hydrothermal Vent Deposits. Hydrothermal Vent Fluids, Chemistry of. Ice–Ocean Interaction. Iron Fertilization. Nitrogen Cycle. Open Ocean Convection. Plankton. River Inputs. Stable Carbon Isotope Variations in the Ocean. Water Types and Water Masses.

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CONTINUOUS PLANKTON RECORDERS

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Introduction

The Continuous Plankton Recorder (CPR) survey is a synoptic survey of upper-layer plankton covering much of the northern North Atlantic and North Sea. It is the longest running and the most geographically extensive of any routine biological survey of the oceans. Over 4 000 000 miles of towing have resulted in the analysis of nearly 200 000 samples and the routine identification of over 400 species/groups of plankton. Data from the survey have been used to study biogeography, biodiversity, seasonal and inter-annual variation, long-term trends, and exceptional events. The value of such an extensive time-series increases as each year's data are accumulated. Some recognition of the importance of the CPR survey was achieved in 1999 when it was adopted as an integral part of the Initial Observing System of the Global Ocean Observing System (GOOS).

History

The CPR prototype was designed by Alister Hardy for operation on the 1925–27 Discovery Expedition to the Antarctic, as a means of overcoming the problem of patchiness in plankton. It consisted of a hollow cylindrical body tapered at each end, weighted at the front and with a diving plane, horizontal tail fins, and a vertical tail fin with a buoyancy chamber on top (**Figure 1A**). Hardy designed a more compact version with a smaller sampling aperture for use on merchant ships and this was first deployed on a commercial ship in the North Sea in September 1931 (**Figure 1B**). During the 1980s the design was modified further to include a box-shaped double tail-fin that provides better stability when deployed on the faster merchant ships of today (**Figure 1C**). The space within this tail-fin is used in some machines to accommodate physical sensors and flowmeters. The normal maximum tow distance for a CPR is approximately 450 nautical miles (834 km).

By the late 1930s there were seven CPR routes in the North Sea and one in the north-east Atlantic; in 1938 CPRs were towed for over 30 000 miles. After a break for the Second World War, the survey restarted in 1946 and expanded into the eastern North Atlantic. Extension of sampling into the western North Atlantic took place in 1958. The survey reached its greatest extent from 1962 to 1972 when CPRs were towed for at least 120 000 nautical miles annually. Sampling in the western Atlantic, which had been suspended due to funding problems in 1986, recommenced in 1991 and is still ongoing. **Figure 2A** shows the extent of the survey in 1999.

Initially based at the University College of Hull, the survey moved to Leith, Edinburgh in 1950 under the management of the Scottish Marine Biological Association (now the Scottish Association for Marine Science). In 1977 it finally moved to

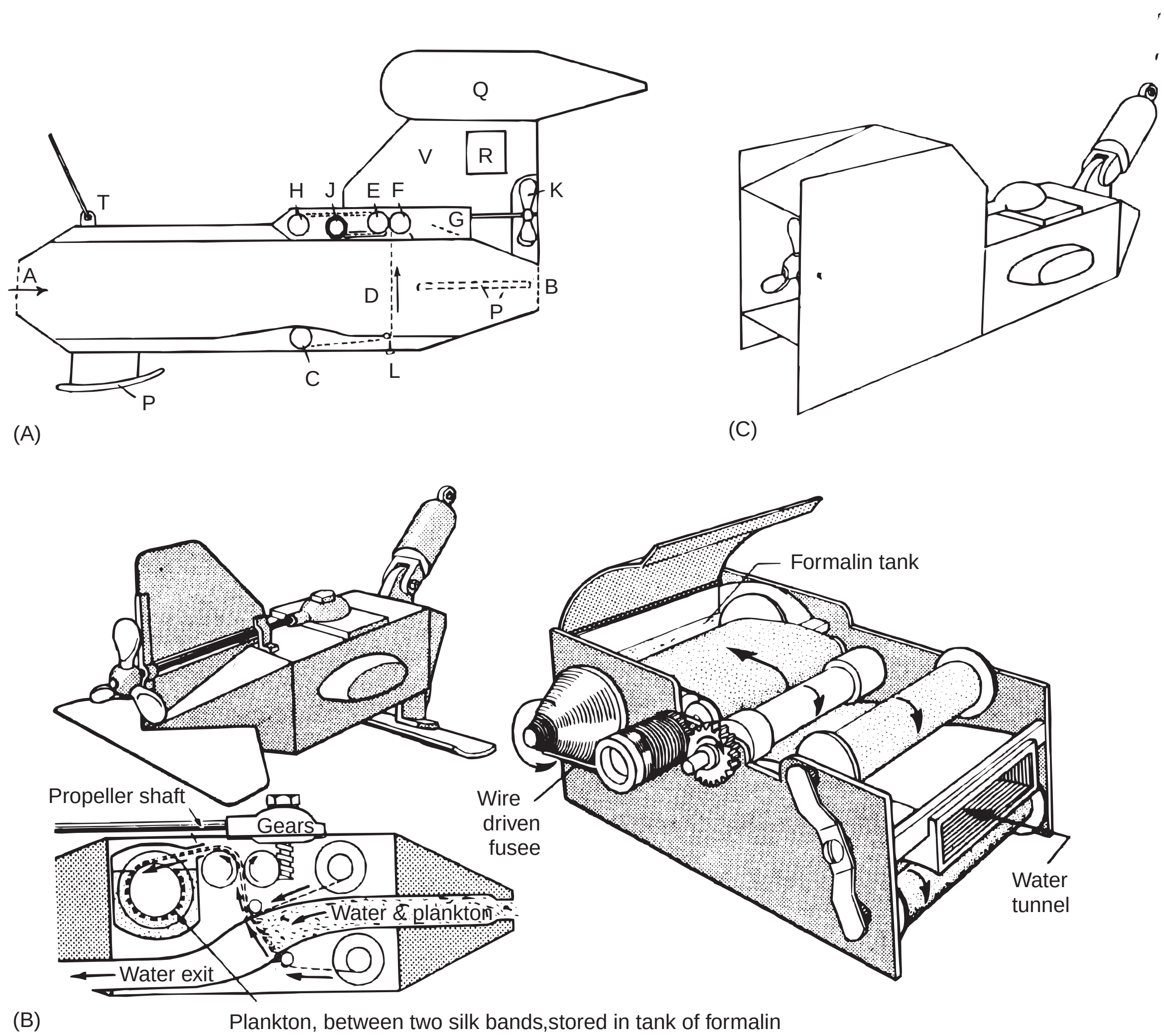

Figure 1 (A) Diagram of the first Continuous Plankton Recorder used on 'Discovery'. (Reproduced with permission from Hardy, 1967). (B) The 'old' CPR, used up to around 1983, showing the internal filtering mechanism. (C) The CPR in current use, with the 'box' tail-fin.

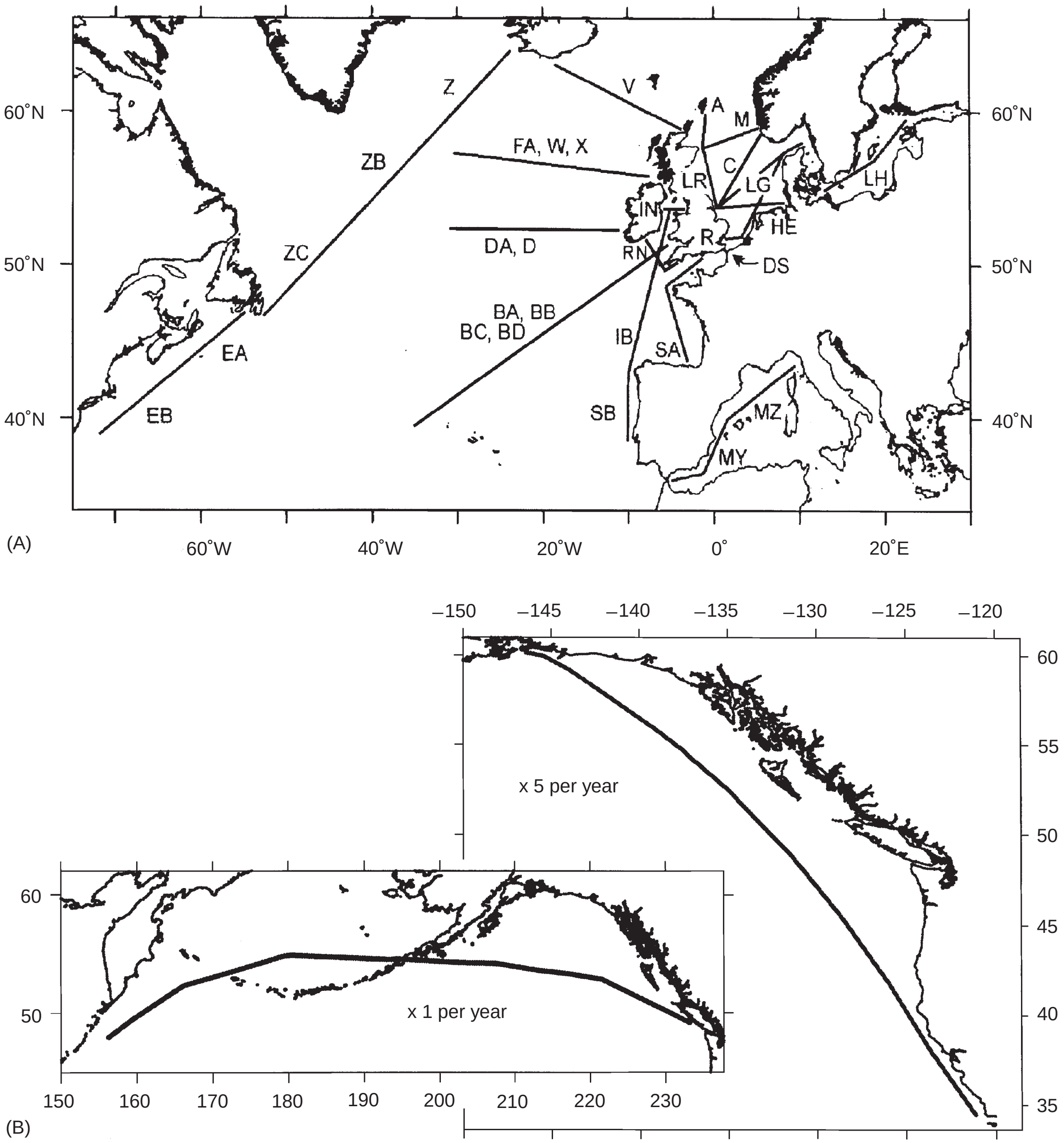

Figure 2 (A) CPR routes in 1999/2000. (B) CPR routes in the Pacific Ocean towed in 2000 and 2001.

Plymouth as part of the Institute for Marine Environmental Research (now Plymouth Marine Laboratory). After a short period of uncertainty in the late 1980s, when the continuation of the survey was threatened, the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) was formed in November 1990 to operate the survey. Since 1931 more than 200 merchant ships, ocean weather ships, and coastguard cutters – known as 'ships of opportunity' – from many nations have towed CPRs in a voluntary capacity to maintain the survey. The Foundation is greatly indebted to the captains and crews of all these towing ships and their shipping and management companies, without whom the survey could not continue.

During the 1990s CPRs were towed by SAHFOS in several other areas, including the Mediterranean (1998–99), the Gulf of Guinea (1995–99), the Baltic (1998–99), and the Indian Ocean (1999). A separate survey by the National Oceanic and Atmospheric Administration/National Marine Fisheries Service using CPRs along the east coast of the USA off

Narragansett has been running since 1974; CPRs are currently towed on two routes in the Middle Atlantic Bight. Following a successful 2000 mile trial tow in the north-east Pacific from Alaska to California in July–August 1997, a 2-year survey by SAHFOS using CPRs in the north-east Pacific started in March 2000. In addition to five tows per year on the Alaska–California route, there is one 3000 mile tow annually east–west from Vancouver to the north-west Pacific (**Figure 2B**). A 'sister' survey, situated in the Southern Ocean south of Australia between 60°E and 160°E, is operated by the Australian Antarctic Division. In this survey CPRs have been deployed since the early 1990s on voyages between Tasmania and stations in the Antarctic.

As the operator of a long-term international survey, which has sampled in most of the world's oceans, SAHFOS regularly trains its own staff in plankton identification. In recent years SAHFOS has also trained scientists from the following 10 countries: Benin, Cameroon, Côte d'Ivoire, France, Finland, Ghana, Italy, Nigeria, Thailand, and the USA.

The Database and Open Access Data Policy

The CPR database is housed on an IBM-compatible PC and stored in a relational Microsoft Access DATABASE system. Spatial and temporal data are stored for every sample analysed by the CPR survey since 1948. This amounts to $>175\,000$ samples, with around 400 more samples added per month. There are more than two million plankton data points in the database, which also contains supporting information, including sample locations, dates and times of samples, a taxon catalog, and analyst details. In the near future it will also hold additional conductivity, temperature, and depth (CTD) data. Routine processing procedures ensure that, despite various operational difficulties, the previous year's data are usually available in the database within 9 months.

In 1999 SAHFOS adopted a new open access data policy, i.e. data are freely available to all users worldwide, although a reasonable payment may be incurred for time taken to extract a large amount of data. The only stipulation is that users have to sign a SAHFOS Data Licence Agreement. Details of the database can be found on the web site: http://www.npm.ac.uk/sahfos/. This site advertises the availability of data and allows requests for data to be made easily.

The CPR Bibliography, which is available on the SAHFOS web site, lists over 500 references using results from the survey. During the early years many of the papers based on CPR data were published in the 'in-house' journal *Hull Bulletins of Marine Ecology*, which from 1953 onwards became the *Bulletins of Marine Ecology*; this was last published in 1980.

Methods

Merchant ships of many nations tow CPRs each month along 20–25 standard routes (**Figure 2A**) at a depth of 6–10 m. Water enters the CPR through a 12.7 mm square aperture and travels down a tunnel that expands to a cross-section of 50×100 mm, where it passes through a silk filtering mesh with a mesh size of approximately 280 μm. The movement of the CPR through the water turns a propeller that drives a set of rollers and moves the silk across the tunnel. At the top of the tunnel the filtering silk is joined by a covering silk and both are wound onto a spool located in a storage chamber containing formaldehyde solution. The CPRs are then returned to SAHFOS in Plymouth for examination. The green coloration of each silk is visually assessed by reference to a standard color scale; this is known as 'Phytoplankton Color' and gives a crude measure of total phytoplankton biomass. The silks are then cut into sections corresponding to 10 nautical miles (18.5 km) of tow and are distributed randomly to a team of 10–12 analysts. The volume of water filtered per 10-nautical-mile sample is approximately $3\,m^3$. Phytoplankton, small zooplankton (<2 mm in size) and larger zooplankton (>2 mm) are then identified and counted in a three-stage process. Over 400 different taxa are routinely identified during the analysis of samples and the recent expansion of the survey into tropical waters and the Pacific Ocean will certainly increase this figure.

A detailed and thorough quality control examination is carried out by the most experienced analyst on the completed analysis data. Apparently anomalous results are rechecked by the original analyst and the data are altered accordingly where necessary. This system ensures consistency of the data and acts as 'in-service' training for the less experienced analysts.

Instrumentation

On certain routes CPRs carry additional equipment to obtain physical data. In the past temperature has been recorded on certain routes in the North Sea using Braincon™ recording thermographs, prototype electronic packages, and Aquapacks™.

Aquapacks record temperature, conductivity, depth, and chlorophyll fluorescence. These are now deployed on CPR routes off the eastern coast of the USA, in the southern Bay of Biscay and, until November 1999, in the Gulf of Guinea. Vemco™ minilogger temperature sensors are used on routes from the UK to Iceland, and from Iceland to Newfoundland. In order to measure flow rate through the CPR, electromagnetic flowmeters are used on some routes. Such recording of key physical and chemical variables simultaneously with abundance of plankton enhances our ability to interpret observed changes in the plankton.

Results and Applications of the Data

The long-term time-series of CPR data acts as a baseline against which to measure natural and anthropogenic changes in biogeography, biodiversity, seasonal variation, inter-annual variation, long-term trends, and exceptional events. The results have applications to studies of eutrophication and are increasingly being applied in statistical analysis of plankton populations and modeling. Some examples are given below.

Another possible application, in the context of the new Pacific CPR programme, is an inter-comparison with data from the CalCOFI Program, the only other existing decadal-scale survey in the world sampling marine plankton. This survey has taken monthly or quarterly net samples from 1949 to the present over an extensive grid of stations off the west coast of California. In the majority of samples the zooplankton has been measured only as displacement volume, rather than being identified to species, but concurrently measured physical and chemical data are more extensive.

Biogeography of Marine Plankton

Much of the early work of the survey focused on biogeography. Using Principal Component Analysis, Colebrook was able to distinguish five main geographical distribution patterns in the plankton – northern oceanic, southern oceanic, northern intermediate, southern intermediate, and neritic. Two closely related species of calanoid copepod – *Calanus finmarchicus* and *C. helgolandicus* – which co-occur in the North Atlantic and are morphologically very similar, show very different distributions (**Figure 3**). *C. finmarchicus* is a cold-water species whose center of distribution lies in the north-west Atlantic gyre and the Norwegian Sea ('northern oceanic'). In contrast, *C. helgolandicus* is a warm–temperate water species occurring in the Gulf Stream, the Bay of Biscay and the North Sea ('southern intermediate'). These different distribution patterns are reflected in their life histories; *C. finmarchicus* overwinters in deep waters off the shelf edge, whereas *C. helgolandicus* overwinters in shelf waters.

A new species of marine diatom, *Navicula planamembranacea* Hendey, was first described from CPR samples taken in 1962. The species was found to have a wide distribution in the western North Atlantic from Newfoundland to Iceland.

An atlas of distribution of 255 species or groups (taxa) of plankton recorded by the CPR survey between 1958 and 1968 was published by the Edinburgh Oceanographic Laboratory in 1973. An updated version of this atlas, covering more than 40 years of CPR data and over 400 taxa, is in preparation.

Phytoplankton, Zooplankton, Herring, Kittiwake Breeding Data, and Weather

A study in the north-eastern North Sea found that patterns of four time-series of marine data and weather showed similar long-term trends. Covering the period 1955–87, these trends were found in the abundance of phytoplankton and zooplankton (as measured by the CPR), herring in the northern North Sea, kittiwake breeding success (laying date, clutch size, and number of chicks fledged per pair) at a colony on the north-east coast of England, and the frequency of westerly weather (**Figure 4**). The mechanisms behind the parallelism in these data over the 33-year period are still not fully understood.

Calanus and the North Atlantic Oscillation

The North Atlantic Oscillation (NAO) is a large-scale alternation of atmospheric mass between subtropical high surface pressure, centred on the Azores, and subpolar low surface pressures, centred on Iceland. The NAO determines the speed and direction of the westerly winds across the North Atlantic, as well as winter sea surface temperature. The NAO index is the difference in normalized sea level pressures between Ponta Delgadas (Azores) and Akureyri (Iceland). There is a close association between the abundance of *Calanus finmarchicus* and *C. helgolandicus* in the north-east Atlantic and this index (**Figure 5**). At times of heightened pressure difference between the Azores and Iceland, i.e. a high, positive NAO index, there is low abundance of *C. finmarchicus* and high abundance of *C. helgolandicus*; during a low, negative NAO index the reverse is true. However, since 1995 this strong *Calanus*/NAO relationship has broken down and the causes of this are presently unknown. It suggests

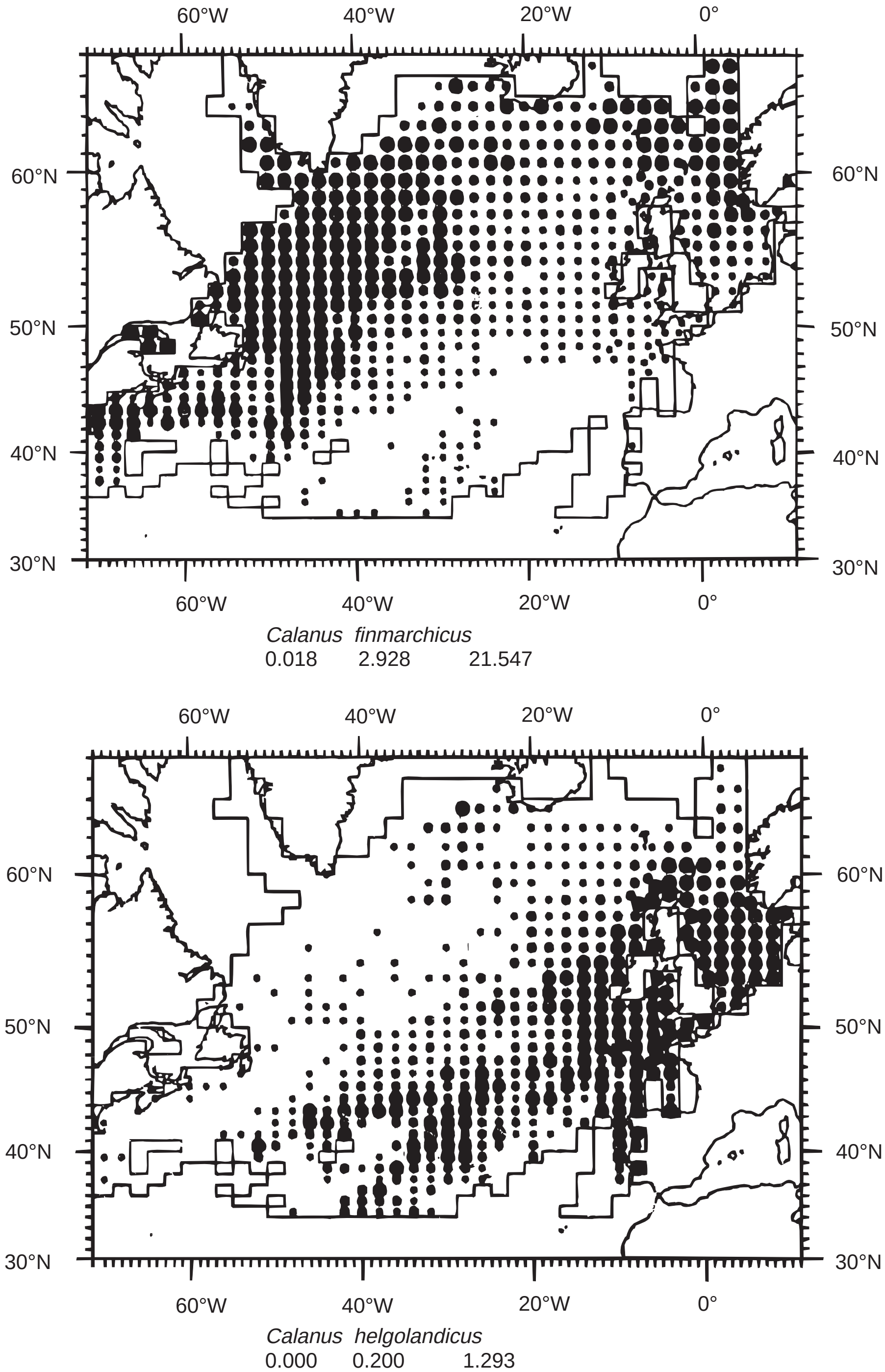

Figure 3 Distribution of *Calanus finmarchicus* and *C. helgolandicus* recorded in CPR samples from 1958 to 1994.

a change in the nature of the link between climate and plankton in the north-east Atlantic.

North Sea Ecosystem Regime Shift

Recent studies have shown changes in CPR Phytoplankton Color, a visual assessment of chlorophyll, for the north-east Atlantic and the North Sea. In the central North Sea and the central north-east Atlantic an increased season length was strikingly evident after the mid-1980s. In contrast, in the north-east Atlantic north of 59°N Phytoplankton Color declined after the mid-1980s (**Figure 6**). These changes in part appear to be linked to the recent high

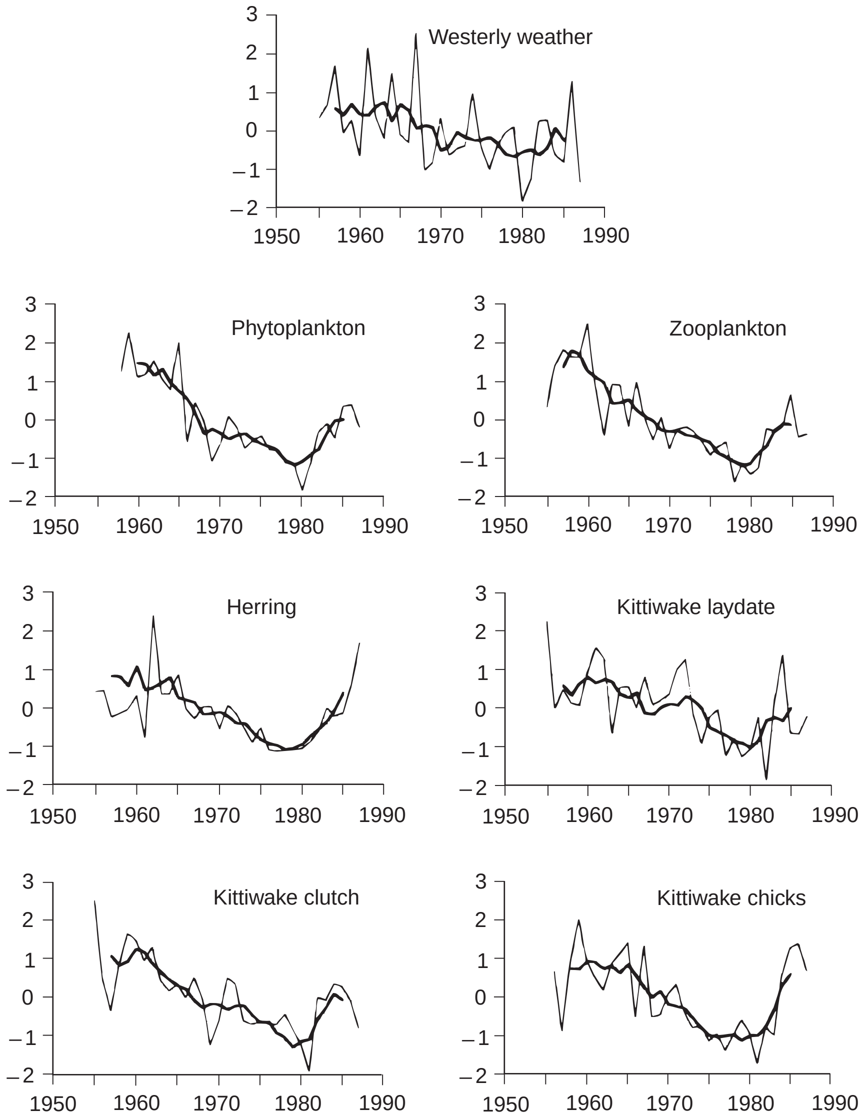

Figure 4 Standardized time-series and 5-year running means for frequency of westerly weather, and for abundances of phytoplankton, zooplankton, herring, and three parameters of kittiwake breeding (laying date, clutch size, and number of chicks fledged per pair), from 1955 to 1987. (Reproduced with permission from Aebischer NJ *et al.* (1990) *Nature* 347: 753–755.)

positive phase of the NAO index and reflect changes in mixing, current flow, and sea surface temperature. The increase in Phytoplankton Color and phytoplankton season length after 1987 coincided with a large increase in catches of the western stock of horse mackerel *Trachurus trachurus* in the northern North Sea, apparently connected with the increased transport of Atlantic water into the North Sea. From 1988 onwards the NAO index increased to the highest positive level observed in the twentieth century. Positive NAO anomalies are associated with stronger and more southerly tracks of the westerly winds and higher temperatures in western Europe. These changes coincided with a series of other changes that affected the whole North Sea ecosystem, affecting many trophic levels and indicating a regime shift.

North Wall of the Gulf Stream and Copepod Numbers

Zooplankton populations in the eastern North Atlantic and the North Sea show similar trends to variations in the latitude of the north wall of the Gulf Stream, as measured by the Gulf Stream North Wall (GSNW) index, which is statistically related to the NAO 2 years previously. **Figure 7** shows the close correlation between total copepods in the central North Sea and the GSNW index. This relationship is also evident in zooplankton in fresh-

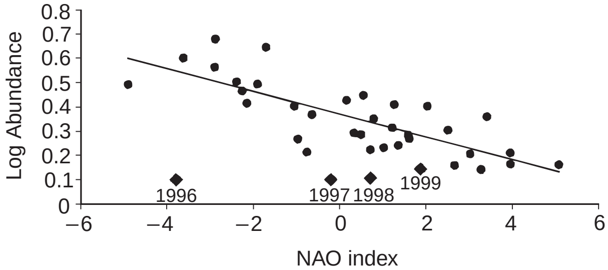

Figure 5 Annual log abundance of *Calanus finmarchicus* in the north-east Atlantic Ocean against the NAO winter index for the period 1962–99. (Adapted with permission from Fromentin JM, and Planque B (1996) *Marine Ecology Progress Series* 134: 111–118.)

water lakes and in the productivity of terrestrial environments, indicating a possible climatic control.

Biodiversity

Analyses of long-term trends in biodiversity of zooplankton in CPR samples indicate increases in diversity in the northern North Sea. This may be related to distributions altering in response to climatic change as geographical variation in biodiversity of the plankton shows generally higher diversity at low latitudes than at high latitudes. Calanoid copepods are the dominant zooplankton group in the North Atlantic and the large data set from the CPR survey has been used to map their diversity. This has demonstrated a pronounced local spatial variability in biodiversity. Higher diversity was found in the Gulf Stream extension, the Bay of Biscay, and along the southern part of the European shelf. Cold water south of Greenland, east of Canada, and west of Norway was found to have the lowest diversity (**Figure 8**).

Monitoring for Nonindigenous and Harmful Algal Blooms

The regularity of sampling by the CPR enables it to detect changes in plankton communities. Few case histories exist that describe the initial appearance and subsequent geographical spread of nonindigenous species. In 1977 the large diatom *Coscinodiscus wailesii* was recorded for the first time off Plymouth, when mucilage containing this species was found to be clogging fishing nets. *C. wailesii* was previously known only from southern California, the Red Sea, and the South China Sea and it is believed that it arrived in European waters via ships' ballast water. Since then the species has spread throughout north-west European waters and has become an important contributor to North Sea phytoplankton biomass, particularly in autumn and winter. Such introduced species can, on occasions, have considerable ecological and economic effects on regional ecosystems.

There has been an apparent worldwide increase in the number of recorded harmful algal blooms and

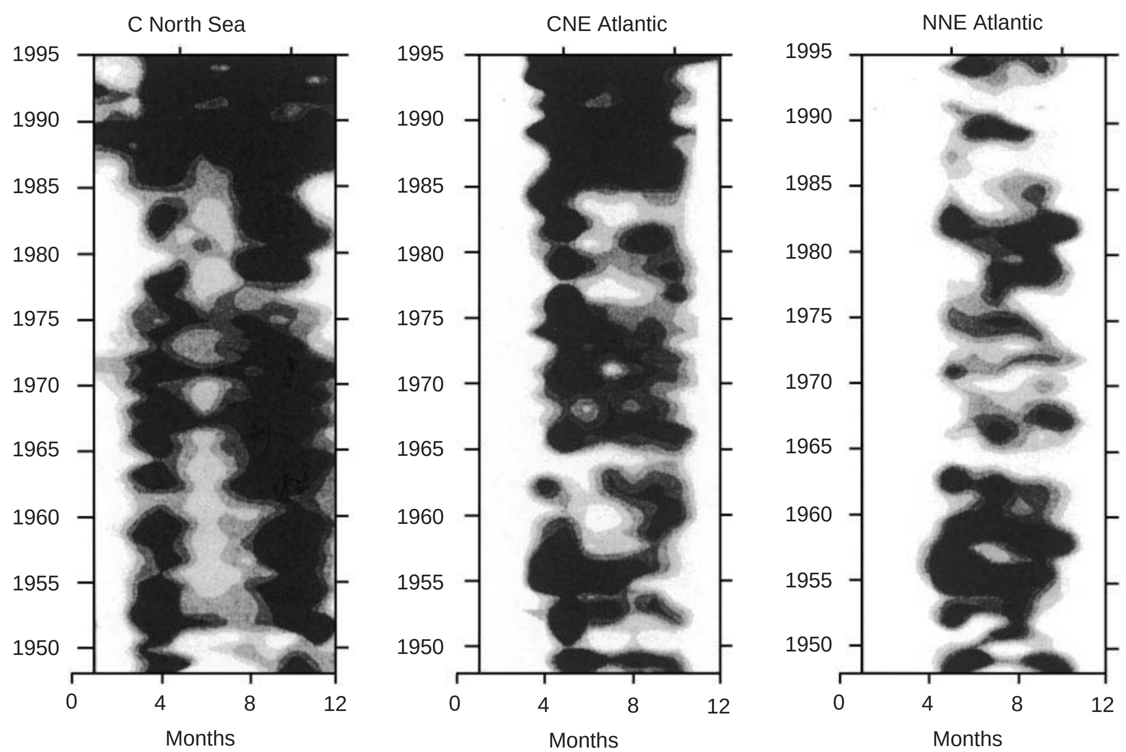

Figure 6 Contour plots of mean monthly Phytoplankton Color during 1948–95 for the central North Sea, and for the central and northern north-east Atlantic. (Reproduced with permission from Reid PC *et al.* (1998) *Nature* 391: 546.)

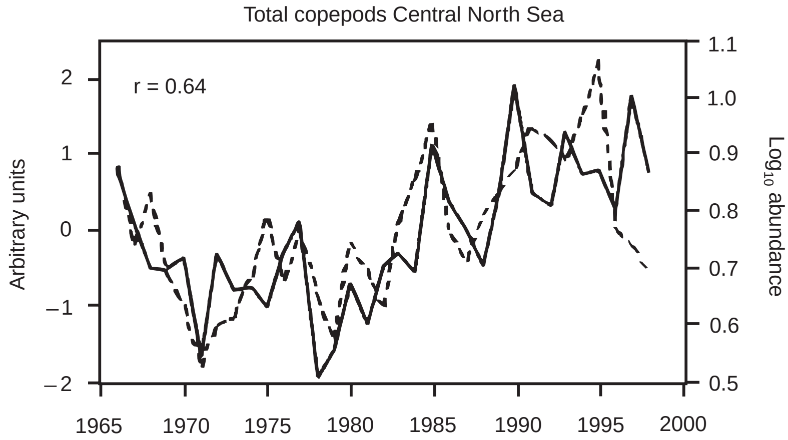

Figure 7 The latitude of the Gulf Stream (the GSNW index 'arbitrary units', broken line) compared with the abundance of total copepods in the central North Sea (solid line). Adapted with permission from Taylor AH *et al.* (1992) *Journal of Mar. Biol. Ass.* UK 72:919–921.

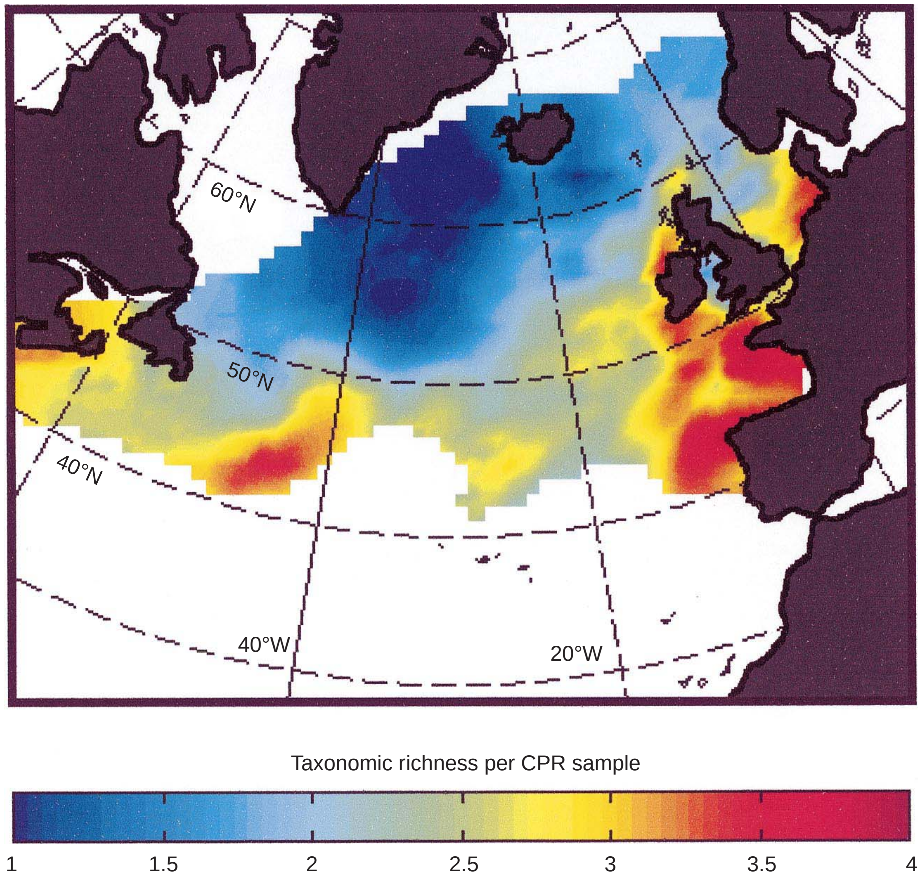

Figure 8 The biodiversity (taxonomic richness) of calanoid copepods in the CPR sampling area. (Adapted with permission from Beaugrand *et al.* (2000) *Marine Ecology Progress Series* 204: 299–303.)

the CPR survey is ideally placed to monitor such events. The serious outbreak of paralytic shellfish poisoning that occurred in 1968 on the north-east coast of England was shown by CPR sampling to have been caused by the dinoflagellate *Alexandrium tamarense*.

Increased nutrient inputs into the North Sea since the 1950s have been linked with an apparent increase in the haptophycean alga *Phaeocystis*, particularly in Continental coastal regions where it produces large accumulations of foam on beaches. In contrast, long-term records (1946–87) from the CPR survey, which samples away from coastal areas, show that *Phaeocystis* has declined considerably in the open-sea areas of the north-east Atlantic and the North Sea (**Figure 9**). It is notable that the decline occurred both in areas not subject to anthropogenic nutrient inputs (Areas 1 and 2, west of the UK) and in the most affected area (Area 4, the southern North Sea). This decrease in *Phaeocystis* up to 1980 is also shown by many other species of plankton, suggesting a common causal relationship.

Exceptional Events

Doliolids are indicators of oceanic water and in CPR samples are normally found to the west and south-west of the British Isles; they occur only sporadically in the North Sea and are rarely recorded in the central or southern North Sea. On two occasions in recent years, in October–December 1989 and September–October 1997, the doliolid *Doliolum nationalis* was recorded in CPR samples taken in the German Bight, accompanied by other oceanic indicator species, suggesting a strong influx of north-east Atlantic water into the North Sea. Both these occasions coincided with higher than average sea surface temperature and salinities.

Summary and the Future

The long-term time-series of CPR data have been used in many different ways:

- mapping the geographical distribution of plankton
- a baseline against which to measure natural and anthropogenically forced change, including eutrophication and climate change
- linking of plankton and environmental forcing
- detecting exceptional events in the sea
- monitoring for newly introduced and potentially harmful species.

In the future new applications of CPR data may include:

- use as 'sea-truthing' for satellites

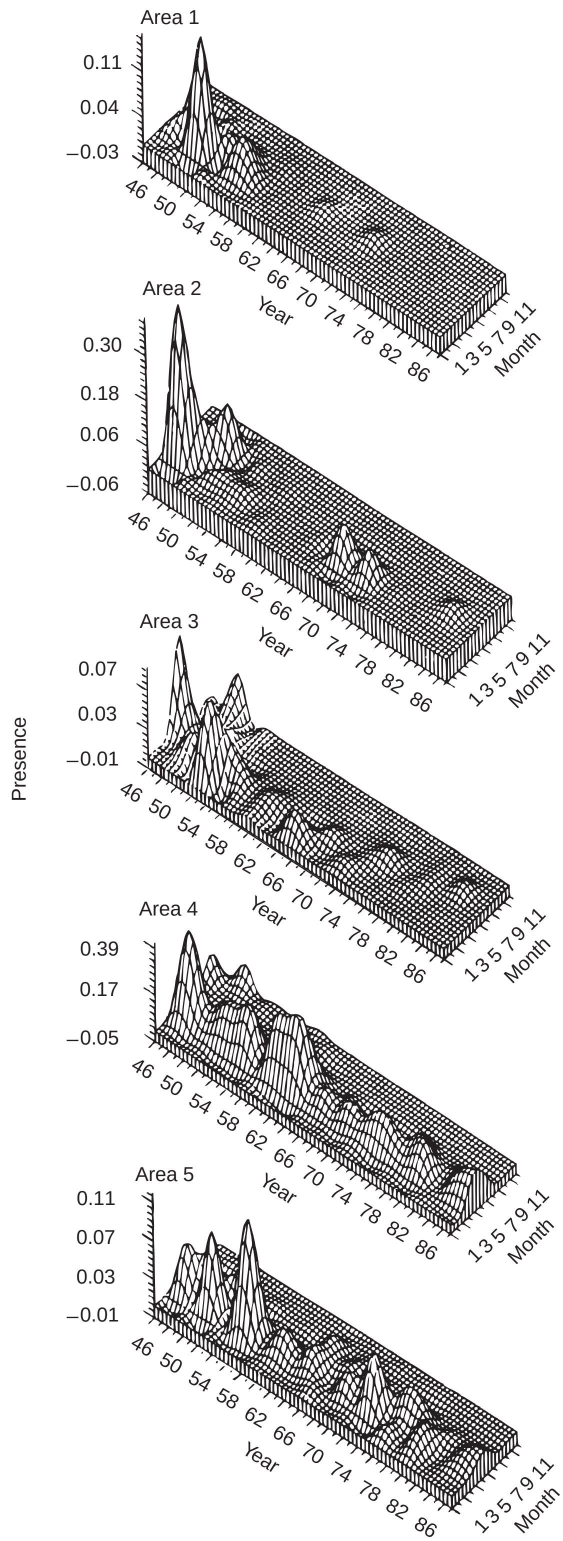

Figure 9 Presence of *Phaeocystis* in five areas of the north-east Atlantic Ocean and the North Sea. Data are plotted for each month for 1946–87 inclusive. (Reproduced with permission from Owens NJP *et al*. (1989) *Journal of Mar. Biol. Ass. UK* 69: 813–821.)

- regional assessment of plankton biodiversity
- regional studies of responses to climate change
- as input variables to predictive modeling for fish stock and ecosystem management
- for construction and validation of new models comparing ecosystems of different regional seas.

The CPR survey has gathered nearly 70 years of data on marine plankton throughout the North Atlantic Ocean, and has recently extended into the North Pacific Ocean. Alister Hardy's simple concept in the 1920s has succeeded in providing us with a unique and valuable long-term data set. There is increasing worldwide concern about anthropogenic effects on the marine ecosystem, including eutrophication, overfishing, pollution, and global warming. The data in the CPR time-series is being used more and more widely to investigate these problems and now plays a significant role in our understanding of global ocean and climate change.

See also

Climate and Plankton. Copepods. Diversity of Marine Species. Ecosystem Effects of Fishing. Eutrophication. Exotic Species, Introduction of. Fish Larvae. Florida Current, Gulf Stream and Labrador Current. Gelatinous Zooplankton. Large Marine Ecosystems. North Atlantic Oscillation (NAO). North Sea Circulation. Ocean Colour from Satellites. Pelagic Fish. Phytoplankton Blooms. Plankton. Protozoa, Planktonic Foaminifera. Protozoa, Radiolarians. Satellite Remote Sensing of Sea Surface Temperatures. Shelf-sea and Slope Fronts.

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CONVECTION

See **DEEP CONVECTION; DOUBLE-DIFFUSIVE CONVECTION; OPEN OCEAN CONVECTION**

COPEPODS

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Introduction

Copepods are microscopic members of the phylum Crustacea, the taxonomic group that includes crabs, shrimps and lobsters and is the only large class of arthropods that is primarily aquatic. The name copepod comes from the Greek words *kope* (an oar) and *podos* (foot), the majority of members of the group having five pairs of flat paddlelike swimming legs. About 10 000 species are currently known, and their numerical dominance as members of the marine plankton means that they are probably the most numerous metazoan – multicellular – animals on earth. In addition to forming a major component of marine plankton communities, copepods are also found in sea-bottom sediments, as well as associated with many marine plants and animals. They play