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The Continuous Plankton Recorder: concepts and history, from Plankton Indicator to undulating recorders

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Abstract

Alister Hardy conceived the Continuous Plankton Recorder (CPR) survey in the 1920s as a means of mapping near-surface plankton in space and time, interpreting the changing fortunes of the fisheries and relating plankton changes to hydrometeorology and climatic change. The seed he planted has grown to become the most extensive long-term survey of marine organisms in the world and the breadth of his vision becomes ever more apparent. The survey has now run for over 70 years and its value increases with every passing decade. Operating from ‘ships of opportunity’ the machines used are robust, reliable and easy to handle. Wherever possible, all the sampling and analytical methods have not been changed to maintain the consistency of the time series. Computerisation and the development of new statistical approaches have increased our ability to handle the large quantities of information generated and enhance the sensitivity of the data analyses. This overview, based on almost 900 papers, recounts the various phases in the history of the survey. It starts with the Indicator Survey (1921–1934), the deployment of the first CPR on the Discovery Expedition (1924–1927) and the early CPR survey in the North Sea (1931–1939). The survey reopened in 1946 after the Second World War and expanded across the North Atlantic to North America from 1959. Taxonomic studies were initiated and an emphasis was placed on patterns of distribution, which were seen to reflect the varying oceanographic conditions. The years 1968–1976 saw further expansion with operations even in the American Great Lakes, publication of a Plankton Atlas and initial evidence for a downward trend in plankton biomass. At about this time electronic instrumentation was attached to CPRs to make additional measurements and work was started on the development of a new generation of undulating Continuous Plankton and Environmental Recorders (CPERs). In 1976 the survey moved to Plymouth. Scientific priorities in the UK changed in the subsequent decade and funding became more difficult to secure even though some of the CPR papers being published at the time are now regarded as classics in plankton ecology. In 1988 the UK Natural Environment Research Council (NERC) decided to close the survey. An international rescue operation led to the creation of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in 1990, which has continued with consortium funding from a number of countries, and from 1999 again included NERC. The scientific

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rationale of the survey has gained credibility as concern over climate change and other anthropogenic effects has grown and as the key role that plankton plays as an indicator of large-scale environmental conditions becomes ever more apparent. Recently, the survey became an integral component of the Global Ocean Observation System (GOOS) and expanded into the North Pacific. It plays a complementary role in many large international and multidisciplinary projects and is providing inspiration, advice and support to daughter surveys elsewhere in the world. At the start of a new millennium, Hardy's vision from the 1920s is a powerful driving force not just in international biological oceanography, but in global environmental science.

Keywords: Continuous Plankton Recorder (CPR); Phytoplankton; Zooplankton; Time series; Biogeography; Oceanographic instrumentation; North Sea; North Atlantic; North Pacific

Contents

1. Introduction

The Continuous Plankton Recorder (CPR) survey is one of the longest running marine biological surveys in the world, and certainly the most comprehensive. Our present understanding of the dynamics of plankton at the scale of an ocean basin, over monthly seasonal cycles and in the time-frame of decadal change would not have been achieved without it (Brander, Dickson and Edwards, this volume). The unique operational products of the survey have also provided practical applications to a wide range of policy issues, such as eutrophication, biodiversity and climate change.

By the end of 2001, almost 900 scientific papers had been written that make use of CPR results. Part of this literature was reviewed by Olson, Odlaug and Swain (1966) and Radach (1984). A bibliography in the form of a searchable database using the software EndNote and as HTML listings in alphabetical and chronological order is now available on the web site (http://www.sahfos.org) of the Sir Alister Hardy Foundation for Ocean Science (SAHFOS).

The wide geographical coverage of the survey has been possible through the enormous contribution of the many voluntary ‘ships of opportunity’ (SOOP) that have towed CPR machines, involving close to 250 vessels from more than 30 nations. The vessels have included weather, naval, hydrographic and research ships, ferries and a wide range of other merchant ships ranging in size from ~265 to 220,000 tonnes. In 2001, the survey routinely operated on 24 routes each month extending from 35° to 64°N and 11°E to 72°W in the North Atlantic, as well as across the North Pacific on two less regular, but long routes. We are greatly indebted to the many owners, captains, crew and shore-based personnel who have contributed to the work of the survey over the last 70 years.

Since the first CPR tow in the North Sea in 1931 by Alister Hardy, the methodology (Warner & Hays, 1994) has been used in all the oceans of the world, as well as in the North Sea, the Mediterranean, the Baltic, and in freshwater lakes. However, the core CPR programme of monthly, synoptic sampling has focused on the northwest European shelf and in the Northeast and Northwest Atlantic. A new SAHFOS survey started to operate routinely in the North Pacific in 2000, and sister surveys, using a similar methodology, now operate from Narragansett, USA and Tasmania, Australia.

More than four million miles of CPR tows at a depth of ~10 m (Fig. 1) have been carried out since 1931, with the highest concentration of sampling in the North Sea and Northeast Atlantic. Close to 190,000 samples have been analysed under microscopes (Fig. 1), when phytoplankton and zooplankton are counted and identified into ~500 different taxa. Double the number of analysed samples have been archived and are available for further research. The computerised database for this unique survey contains observations from an average of ~20 ship routes per month since 1946. To improve access to this information, and as part of the Initial Observing System of the Global Ocean Observing System (GOOS), an open-data policy has been implemented. Applications for data should be made to the SAHFOS data manager.

In the course of its history the survey has operated from Hull, Edinburgh and Plymouth. It was initially attached to the University College of Hull. It moved to Edinburgh in 1950 when it came under the auspices of the Scottish Marine Biological Association, and was subsequently transferred to the Institute for Marine Environmental Research (IMER), now the Plymouth Marine Laboratory (PML) in 1976. Its final move was to the Citadel Hill Laboratory, Plymouth, on the establishment of SAHFOS in 1990.

Until 1990, the survey’s funding came from a variety of UK governmental sources, and was supplemented in the 1960s by a contribution from the USA to establish a survey in the western Atlantic. Between 1991 and 2002, funding for SAHFOS has derived from an international consortium, which in

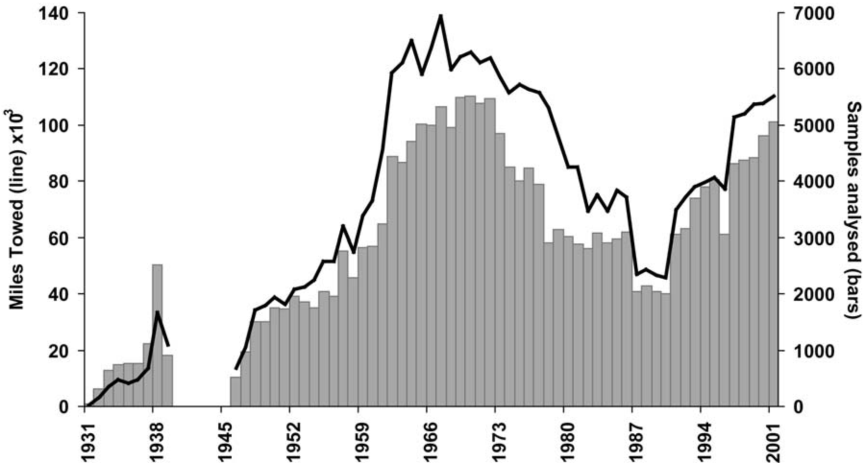


Fig. 1. Towed CPR mileage and samples analysed 1931–2001.

recent years has included: the Intergovernmental Oceanographic Commission (IOC), United Nations Industrial Development Organisation (UNIDO), Canada, Denmark, Faroe Islands, France, Finland, Iceland, Ireland, The Netherlands, Portugal, UK, USA, The Atlantic Salmon Trust and WWF.

When he undertook the first CPR tows in the 1930s, Hardy's vision was to map the distribution of plankton synoptically at monthly intervals and integrated over a scale of nautical miles. He wished to apply to the biology of the North Sea the same approach as weather forecasters in order to produce information that could benefit the economic performance of the fishery. Hardy intended that the survey should be used to evaluate changes in hydrography and climate and so provide information for a marine phenology. At the time he did not expect that the survey would continue over decades, as funding agencies do not normally think beyond 3 years ahead. The survival of the survey for over 70 years is a reflection of its continuing and increasing value as a basis for government policy decisions; after this long period Hardy's vision is coming to fruition.

The long-term consistency of the instrumentation, the methodology and the procedures used in plankton analysis give the results a unique quality. This stamp of assurance gives confidence in the reliability of the data, in particular the reality of the decadal changes in the abundance and distribution of the plankton observed over more than five decades.

In this paper we attempt to synthesise the results of the survey based on a review of close to 1000 publications. Our analysis shows growing sophistication in the interpretation of the database through time. This paper gives the historical background to the survey, including the development of its precursor, the Indicator Survey. Information is provided on the various phases of instrument development, followed by sampling methods, plankton analysis and data processing. The main research findings from each historical period are outlined, and a section of the paper presents the development and application of new technology to the survey, either as additional instrumentation attached to the CPR or as new towed bodies (Continuous Plankton and Environment Recorders (CPERs)). These instruments measure a range of environmental variables as well as sampling plankton, and have different sampling characteristics, such as undulation. A final section provides some thoughts on the future direction of the survey over the next 70 years.

2. How the CPR survey started

In the 1920s the east-coast drift-net herring fishery was of major economic importance to the United Kingdom (Hardy, 1959). Hundreds of drifters were following the herring shoals as they migrated south to their spawning grounds each year. There were large interannual fluctuations in the size and location of catches and it was recognised that an improved understanding of their planktonic food might help explain this variability and improve the efficiency of the fishery (Hardy, 1956). Alister Hardy was appointed as an assistant naturalist in the Fisheries Laboratory, Lowestoft in August 1921 to study these issues. He focused his research on developing an understanding of the diet and feeding habits of North Sea herring at different stages of their life history (Hardy, 1924). At the same time he initiated experiments with the Plankton Indicator, work that can be considered as the precursor of the CPR survey. Much of the subsequent history of the indicator and CPR surveys was closely tied to Hardy's own career and was in large measure a result of his dynamism, forward thinking and practical inventiveness.

Early studies by Hardy in the 1920s were focused on practical problems in the fishery, including the identification of the most productive locations in which to fish. The initial surveys with the Plankton Indicator (Hardy, 1926a) were designed to provide a general definition of spatial variability in the plankton, to map plankton patches and to test the hypothesis of ecological exclusion, whereby the spatial occurrences of one or more types of organism may act as barriers to the penetration of others. Hardy was able to show that migrating and feeding herring appeared to avoid dense blooms of phytoplankton and fed preferentially in denser patches of zooplankton. At an early stage in his work he recognised the need to sample over large space and time scales in order to evaluate changes in the abundance and distribution of plankton. His selection as a member of the Discovery Expedition to Antarctica in 1924 gave him the opportunity—and the necessary financial backing—to design and build the first Continuous Plankton Recorder (CPR) and so turn his concept into a practical reality. The success of the prototype (Fig. 2) on the first leg of the expedition in 1925–1926, when more than 1300 miles of plankton were logged, was reported to *Nature* (Hardy, 1926b). In it Hardy noted that there are marked variations in the density of plankton in different oceanic regions.

On his return from Antarctica and after his appointment as professor of the new Department of Zoology at what was then the University College of Hull, Hardy designed a smaller version of the CPR suitable for operation from merchant ships on their normal routes of passage. Preliminary trials were initiated in 1930 and the first official tow of what was to become the CPR survey was made in September 1931. Alister Hardy assisted with the deployment breaking his finger in the process. Since that one accident, the

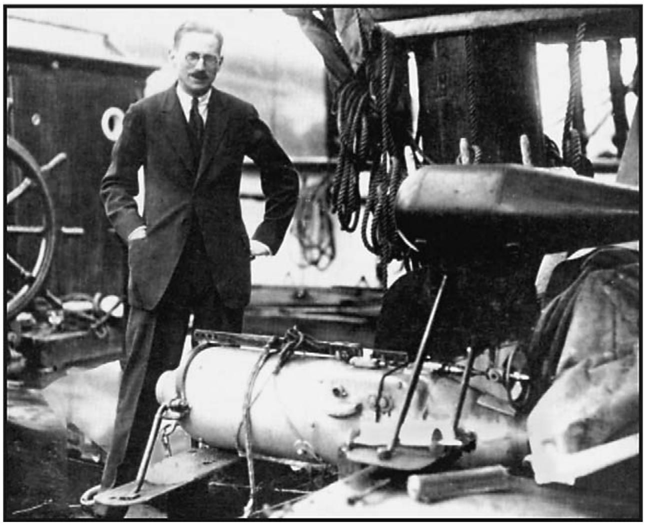


Fig. 2. Alister Hardy and CPR Type I on RRS *Discovery*.

survey has fortunately had a clean safety record. On a routine monthly basis, the operational survey proper started in June 1932 (Hardy, 1939).

In explaining the objectives of the CPR survey and the relevance of the work for the fishing industry, Hardy (1939) made an analogy between the aim to describe plankton changes over large areas and the definition of high and low pressure systems on weather maps. To quote: "The idea underlying the initiation of this ecological survey was that of attempting to apply methods similar to those employed in meteorology to a study of the changing plankton distribution, its causes and effects". Note that it was over three decades later that the existence of mesoscale eddies were recognised in the oceans. Three main objectives were outlined for the survey:

1. To map the distribution of the plankton month by month;
2. To correlate observed temporal and spatial changes in the plankton with the changing fortunes of both the pelagic and demersal fisheries;
3. To correlate changes with 'hydrological' (hydrographic) and climatic change.

In doing this he initiated what is possibly the first operational oceanographic survey, intending that the information acquired would be "a service like that of weather forecasting" to the fishing industry by helping it to operate more economically. It is thus appropriate that the survey was incorporated into the Initial Observing System of the Global Ocean Observing System (GOOS) in 1999. He also foresaw that an improved understanding of the ecology of the North Sea must in time have economic benefit to society. Finally, he considered that the progressive acquisition of information on the timing of biological events would provide a marine phenology, a forecast that has recently come to fruition through the inclusion of CPR material in a phenological analysis of indicators of climate change in the UK (Cannell, Palutikof, & Sparks, 1999).

3. Phases of CPR machine development

On a cruise of the RV *George Bligh* in March 1922 to study the distribution of young herring in the Southern Bight of the North Sea, Hardy unexpectedly found himself in charge owing to the illness of a colleague. With favourable weather and a day to spare, he decided to return to a previous station and carry out sampling at the same place over a 24-h period. This survey illustrated the extreme patchiness of plankton. The variations in the numbers of larval herring caught during this period were greater than those at all the stations occupied during the previous spatial survey over 6 days. To help study this spatial and temporal variation Hardy experimented with a towed tube with an inserted gauze disc that sieved the plankton while the ship was underway. From this initial trial he developed the Plankton Indicator, the precursor of the CPR. Brief accounts of the different phases in the development of the CPR are given below with line drawings of the various models of the CPR and related plankton-sampling devices illustrated in Fig. 3.

3.1. Plankton Indicator

A prototype 'Torpedo Plankton Detector', which sampled the plankton on a disc of 60-mesh silk attached at the rear of a ~4 foot (1.3 m) long tube, was first tested in 1922 and 1923 (Fig. 3). This instrument was deployed on a 60 fathom (110 m) line with a weight of 20 lb (9.1 kg) (Hardy, 1926a). For the more extensive surveys that were carried out from 1930 he designed (Fig. 3) the 'Plankton Indicator Mark II' (Standard Plankton Indicator, patented in August 1922) (Hardy, Lucas, Henderson, & Fraser, 1936). He also designed a 'Miniature Indicator' (Fig. 3) with a sampling disc 1 inch (2.5 cm) in diameter (Hardy,

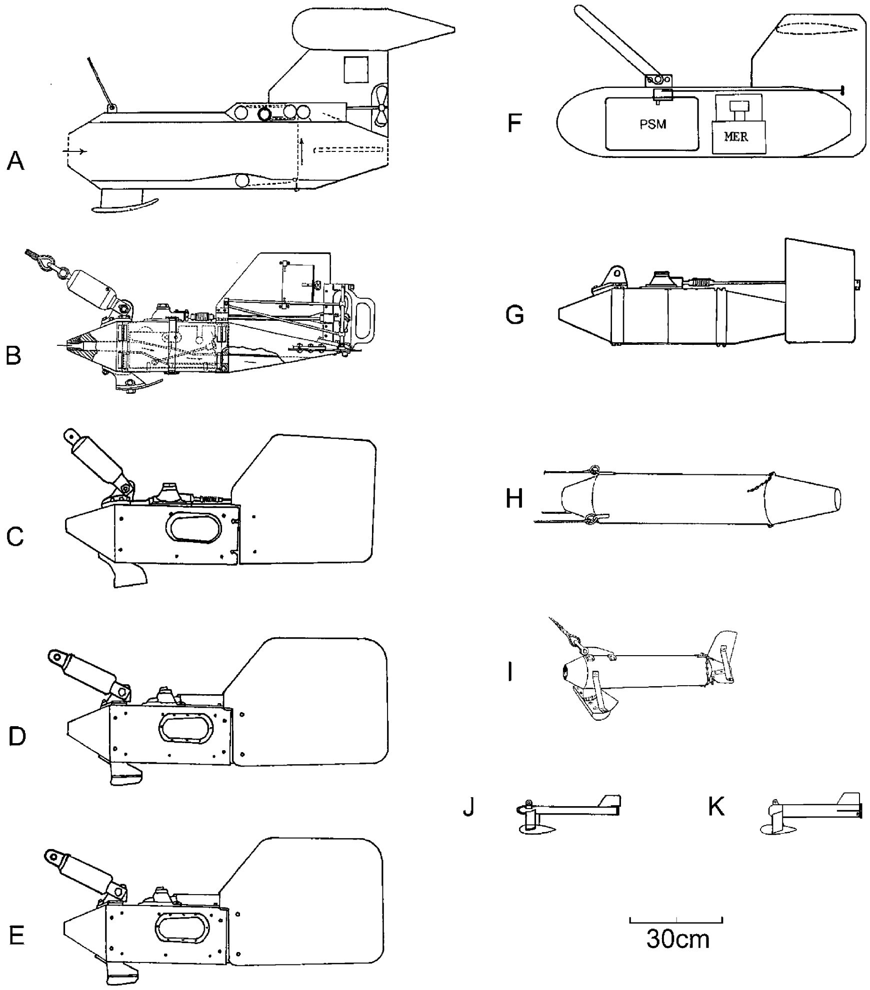


Fig. 3. Scale line drawings of the different types of Continuous Plankton Recorder and Plankton Indicator in side view (A, CPR Type I; B, CPR Type II Mark I; C, CPR Type II Mark II; D, CPR Type II Mark III; E, CPR Type II Mark IV; F, Fast CPR; G, CPR Type II Mark V; H, Prototype Plankton Indicator; I, Plankton Indicator Mark II; J, Miniature Plankton Indicator; K, Plankton Indicator Mark III.

Lucas, Henderson & Fraser, 1936) for studies of relationships between phytoplankton patches and herring in the East Anglian fishery. After the Second World War the 'Plankton Indicator Mark III' (the Small Plankton Indicator) was developed for studies of ecological relationships between plankton and herring off the north-east coast of Scotland. A number of different types of this instrument were produced for sampling at different depths and in conjunction with small nets (Glover, 1953). Methods of analysis used in the various Indicator Surveys are given in the papers cited above and by Bainbridge and Forsyth (1972).

3.2. Continuous Plankton Recorder Type I

While preparing for the 1925–1927 Discovery Expedition to Antarctica, Hardy experimented with a new towed machine to take continuous samples of the plankton on a moving band of silk, the Continuous

Plankton Recorder (CPR) Type I. The plankton from a long, thin square ‘tube’ of water were ‘telescoped’ on to the two-dimensional space of the band of silk gauze for ease of examination under a microscope. The prototype proved unstable and help was sought from the Department of Mine Design, HMS *Vernon*, Portsmouth, in the design of diving planes and weighting. They also provided a table giving the length of towing rope needed to sample at different depths. The final design as used on *Discovery I* (Hardy, 1926b, 1936b) gave perfect stability in tests up to 15 knots. More than 4000 nautical miles were towed during which time many modifications were made to the design; the most successful tow was achieved on return home across Drake Passage (Hardy, 1967). The silk sections were marked with India ink at 6-inch (15 cm) intervals typically representing a tow of 2.3 nautical miles. Each roll of silk was unrolled across a glass stage and examined section by section under a microscope.

3.3. Continuous Plankton Recorder Type II (Marks I–IV)

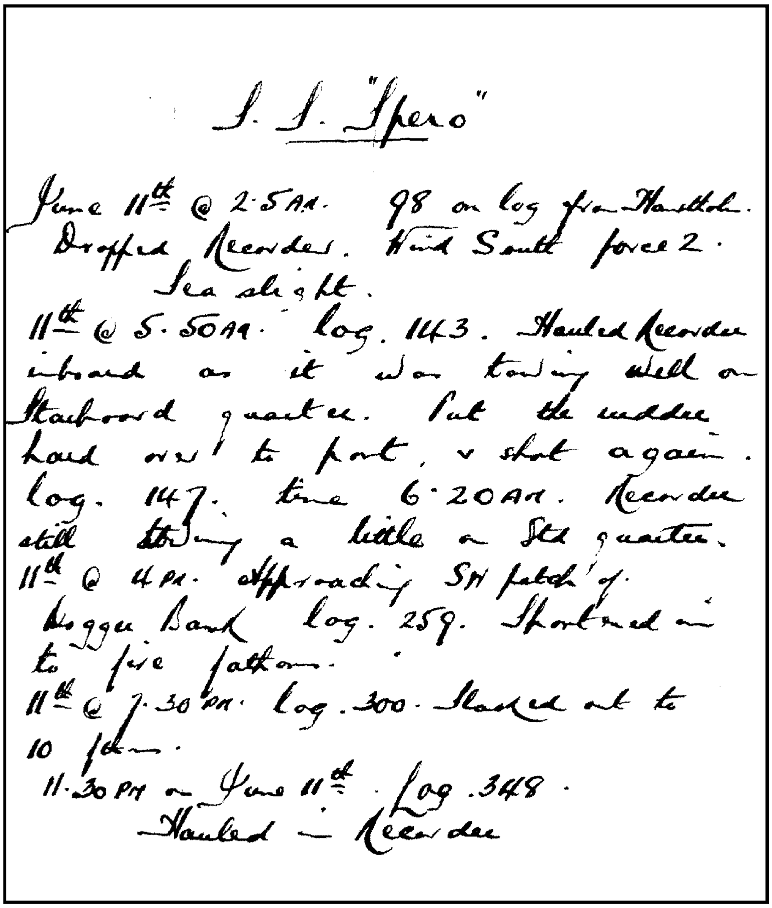
In 1929 Hardy designed a second, smaller version of the CPR in Hull modified to withstand the rigours of deployment from merchant ships of opportunity in all weather conditions (Hardy, 1930, 1935, 1936b). A series of trial tows across the North Sea is believed to have started in 1929 with the results from the first analysed section published in June 1931 (Fig. 20 in Hardy, 1939). The first official tow of the CPR took place on 15 September 1931 from the SS *Albatross*. Regular monthly sampling of the CPR survey began on 11 June 1932 with a tow from the SS *Spero* (Fig. 4). With only minor modifications, described below, the Type II (Mark I) design has remained in service to the present day. The first of the two main changes was necessitated by the rise in ship speeds in the 1970s and the second by the need to carry additional sampling equipment. In November 1977, because of the increasing speeds of many of the ships, the design was modified by the attachment of a box tail to increase towing stability (Fig. 3). The box-tail version of the CPR (Mark II) was introduced progressively, so that by December 1980 most CPRs in use had been modified. The Mark III CPR introduced in May 1985 is a slightly elongated machine with a rear end modified to carry additional electronic sampling packages, such as the ‘Aquapack’ of Chelsea Instruments plc. In 1998 a new Mark IV CPR was introduced, constructed from stainless steel, and based on a computer-aided design (CAD) of the Mark II version.

3.4. Fast Continuous Plankton Recorder (FCPR)

Around 1975 some of the CPRs became unstable under tow, a problem which was traced to the increasing use of high-speed container ships. In the 1950s the ships’ speeds were generally <14 knots, but by 1970 average speeds had risen to >17 knots and some vessels were exceeding 20 knots. As a result, an increasing number of CPRs were lost and the goodwill of the volunteer ship owners, captains and crew was being undermined by the potential dangers of the towing performance. A series of trials was initiated to study the towing and sampling characteristics of CPRs (described later in Section 6) and these led to the design of a new ‘Fast CPR’ (FCPR). The main modifications were the absence of a diving plane and the attachment of twin, large-area, tail fins with an adjustable tail-plane between them. The box tail of CPR (Mark II) evolved from this design. The body of the FCPR was made of glass-reinforced plastic around a stainless-steel frame with overall dimensions comparable to the CPR: length 1.0 m; width 0.4 m; height at tail fin 0.45 m. A forward hold housed a standard CPR Plankton Sampling Mechanism (PSM) cassette and a rear hold was available for instrumentation. Replicate tows by FCPRs of standard monthly CPR deployments were made on the LR route in the North Sea several times throughout 1977.

3.5. Australian CPR Type II (Mark V)

In 1995, the Australian Antarctic Division using CAD designed a new Mark V CPR, which was constructed from marine grade 316 stainless steel and was nickel-plated to reduce corrosion (Hosie, Fukuchi, &


S. S. "Spero"

June 11th @ 2·5AM. 98 on log from Hartlepool.
Dropped Recorder. Wind South force 2.
Sea slight.
11th @ 5·50AM. log. 143. Hauled Recorder
inboard as it was towing well on
Starboard quarter. Put the rudder
hard over to port, & shot again.
log. 147. time 6·20AM. Recorder
still towing a little on Std quarter.
11th @ 4PM. Approaching SW patch of
Dogger Bank log. 259. Shortened in
to five fathoms.
11th @ 7·30PM. log. 300. Slacked out to
10 fathoms.
11·30PM on June 11th. Log. 348.
Hauled in Recorder

Fig. 4. Handwritten log of CPR deployment from the SS *Spero*, June 1932.

Kawaguchi, this volume). The Mark V CPR differs from the Mark II in having a smaller box tail and in the replacement of the characteristic 'side blisters' by streamlined side panels. The PSM cassettes were redesigned for easier loading and unloading of both silk and preservative. In traditional cassettes the preservation bath had to be lifted out to load preservatives as the reservoir plugs are at the front. The new bath is moulded into the back half of the cassette, so that the reservoir is easily accessible and can be filled with preservative without dismantling. Computer-controlled machining and CAD mean that all the various parts, including the cassettes, are now fully interchangeable. In other respects, the Mark V CPR differs little in overall design or performance from earlier versions of the CPR.

4. Methods

4.1. Sampling

In the sampling mechanism of the CPR, plankton is filtered on a band of silk that moves progressively across the flow of water from a small entrance aperture on the nose cone (Hardy, 1939). The speed of water flow is reduced to minimise clogging by an increase in the filtering area of the silk relative to the entrance aperture by a ratio of 29–1. Through a gearing system powered by a small impellor at the rear of the CPR, the silk is moved forward in proportion to the speed of the towing ship, such that typically 4 inches (10 cm) of silk corresponds to 10 nautical miles of tow. The filtering silk and a covering silk are wound together into a storage tank containing formaldehyde for fixation and preservation within a cassette mechanism analogous to that used in a camera. A full cassette of silk can provide up to 450 nautical miles of samples. On longer tows replacement cassettes can be inserted on recovery of the CPR. Further details of the current sampling procedures and processing are given by Warner and Hays (1994). A range of instruments which provide additional measurements have been attached to CPRs over the years. Information on this equipment is given below in Section 6.

Maintaining the CPR survey is a major logistical operation that is only possible through the encouragement and generous assistance provided by many ships and shipping companies. A former ship's captain on the staff of SAHFOS liaises with the ships, ensuring that davits and other tow equipment are adequate for the purpose and comply with appropriate health and safety requirements. Mileage towed and samples analysed (Fig. 2) reached a peak in the late 1960s and early 1970s at more than 120,000 miles and more than 5000 samples analysed per year. After this the survey contracted until 1987 when only some 2000 samples were analysed. Since then, under the operation of SAHFOS, improved coverage has been achieved with a tow mileage of more than 70,000 nautical miles with between 3000 and 5000 samples being analysed per annum. Altogether 181,262 samples have been analysed from 1946 to 2001 inclusive.

4.2. Plankton analysis and changing CPR procedures

1931–1939 Until mid-1937 the aperture at the front of the machine was 3/4 inch (18 mm) square and the silk was moved forward at a slower rate of 1.5 – 2 nautical miles per 2-inch (51 mm) section of silk than is the case at present. In the laboratory, from 1931 to 1936, the silk was slowly unwound as a continuous roll and examined on a specially constructed stage under a traversing microscope (Hardy, 1939). After 1935, the silks were cut on completion of phytoplankton analysis into lengths representing 10 nautical miles of tow (blocks) before zooplankton analysis. All stages of counting plankton were carried out by four analysts. After 1936, the analysts specialised in either phytoplankton, copepods or other zooplankton and divided each analysis accordingly. Other changes that took place in this period included: (a) an experiment with a band of cellophane inserted between the two silks; (b) the introduction of folded edges to the covering silk which successfully reduced squashing of the plankton; and (c) the incorporation of a fusee mechanism into the plankton sampling mechanism (Fig. 5) to compensate for the increasing diameter of the roll of silk as it is wound onto the storage silk. From May 1937 to the present, the size of the aperture was reduced to 0.5 inch (12 mm) square and a faster speed of advance of 5 nautical miles per section of silk was adopted. Methods of analysis from September 1938 were similar to those of the post-war survey, with the exception of *Phaeocystis*, which before the war was measured volumetrically by scraping it from the silk (Lucas, 1941, 1942).

1946–1947 These were years of reappraisal and modification as the mileages increased with the adoption of new routes out into the Atlantic (Rae, 1952). Analytical procedures were simplified, with routine analysis being undertaken by all members of staff and the storage of samples for 'expert' study later as needed. From 1946 onwards only alternate samples were analysed, otherwise the procedures remained the same as prior to the war.

1948–1957 From March 1948 a new four-stage analytical procedure was initiated on alternate samples. The first stage was undertaken by one or more specialists to ensure consistency, and all

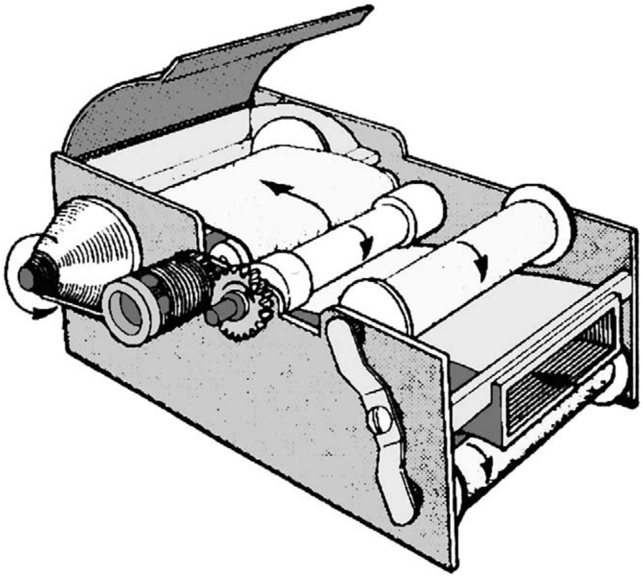


Fig. 5. Drawing of cassette plankton sampling mechanism (PSM) with arrows showing the movement of the silks from the filtering and covering reels to the storage tank. The lid of the tank is open. To the left, indicated by the circular arrow, the fusee mechanism with tightened wire, used to adjust the tension on the rolled up silks.

analysts contributed to subsequent stages (Colebrook, 1960). Apart from the introduction of a new phytoplankton methodology in 1958, this procedure has remained largely unchanged to the present day.

Stage 1 Phytoplankton Colour: Using a standard scale the colour of the silk was assessed into four categories, green, pale green, very pale green and colourless (Robinson & Hiby, 1978).

Stage 2 Phytoplankton analysis: Individual organisms were identified and numbers of each estimated on a 'quasi-logarithmic' scale after examining five microscope fields on both the filtering and covering silks with a magnification of ×450 (×30 objective, ×10 eyepiece, ×1.5 head conversion, field of view 295 μm diameter).

Stage 3 Zooplankton traverse: The number of individuals of small taxa were estimated under a low-power microscope, magnification ×54 (×6 objective, ×6 eyepiece, ×1.5 head conversion, field of view 2.06 mm diameter) into scaled numerical categories along a stepwise traverse across both filtering and covering silk, covering an area 1/40 that of the silk.

Stage 4 Larger zooplankton: Specimens were identified and counted in piles of ~10 individuals.

In the early years of this period, an attempt was made to reduce the acidic action of the silks on the calcareous larvae of bivalves by boiling the silks on certain North Sea routes prior to use and placing a bag of calcium carbonate in the preservation tank of the CPR (Rees, 1951); this practice ceased by 1973.

1958–present In 1958 the phytoplankton methodology (Stage 2) was changed. From this time an estimate of abundance was calculated from the presence or absence of each taxon in 20 'high power'

(1/6 inch objective and ×10 eyepiece) microscope fields, 0.295 mm in diameter chosen along diagonal transects across both the covering and filtering silks, representing one ten-thousandth of the silk (Colebrook, 1960; Robinson & Hiby, 1978).

4.3. Data processing

In the early years of the survey, all data processing was done manually and the results stored in paper form. Calculators were slowly introduced and simple products such as maps, and plots of seasonal and annual cycles were produced, at first along routes and then averaged for statistical areas. In 1969 the first steps were taken to use computers to replace manual data processing and data presentation procedures, a system that became standard in 1971 (Colebrook, 1975). Since that time the computerised database and data processing have undergone a number of iterations (Stevens & Reid, in press), each involving the rewriting of software in different computer languages.

At the present time results are transferred to an Access database housed on a Dell Power Edge Server on completion of plankton analysis and quality control. The database contains more than two million records of plankton taxa for the period 1946–2001. It is split into two sections:

1. Sample information, comprising tow, sample name, longitude, latitude, date/time sample taken; and
2. Plankton information, again with tow name and sample identification plus a taxon identification number and a category of abundance for each taxon.

This system reduces the volume of information to be stored as only positive records are included; if zero values were also included the database would contain more than 80 million data points. A workshop focussing on statistical and time series analyses that could be applied to this large dataset was held in 1993 (Gamble & Edwards, 1996).

In May 1999, SAHFOS Council adopted a new open-access data policy to comply with the requirements of GOOS and to encourage greater use of the data. As part of this policy a data licence agreement has to be signed by each user. Copies of the policy and the data licence can be seen on the SAHFOS web site or requested from the data manager. As a contribution to the Initial Observing Scheme of GOOS monthly mean data for *Calanus finmarchicus* and Phytoplankton Colour averaged for 41 standard areas of the North Atlantic for all months since January 1948 can be downloaded from the SAHFOS web site.

5. History of the Continuous Plankton Recorder Survey

5.1. Incipient years: The Indicator Survey 1921–1924

When Hardy was appointed to the Lowestoft Laboratory in 1921 there was a general belief “that the movements or occurrence of the herring and mackerel at certain seasons are influenced by the presence, in varying degrees, or absence of certain planktonic organisms” (Hardy, 1926a). His work at the time focused on this issue and he drew attention to an association between low catches of herring and ‘weedy water’ containing dense patches of *Rhizosolenia* in his very first paper (Hardy, 1923). It was during this period that he developed the first ‘Plankton Indicator’ using it in a spatial survey carried out in association with the herring drifter fleet (Hardy, 1926a) in what might be considered as the beginnings of the CPR survey.

5.2. An interregnum: The Discovery Expedition 1924–1927

Work with the Plankton Indicator at the Lowestoft laboratory was put on hold following Hardy's appointment in the spring of 1924 to the staff of the Discovery Expedition to Antarctica (Hardy, 1967). His early experience with the indicator had however, given him the idea of designing a machine that could provide a continuous record of plankton mile by mile and to scale, "to enable one to study and compare the uniformity or irregularity of planktonic life in different areas, to measure the size, varying internal density, and frequency of patches, and to indicate more exactly than can be done with comparable tow-net samples whether any correlation exists between different species" (Hardy, 1926b). Over the subsequent months of 1924–1925 he put in hand the design and field trials of the first CPR. The organisation of the expedition was a major logistical exercise and considerable delays occurred in the fitting-out of the ship, which did not finally leave England until September 1925. For the CPR this proved to be fortuitous as the first trials with the initial design proved unstable in the water. On the voyage the CPR was used as an exploratory tool to supplement standard deployments of tow nets during the expedition. A total of 35 records were described in the Discovery reports (Hardy, 1936a) with the most successful transect being taken across the Drake Passage on the return journey (Fig. 6). At the time, Hardy's intention, other than the general aims described earlier, was to confirm that plankton is unevenly distributed in the ocean, and hence resolve the opposing arguments of the Haeckel and Hensen schools of plankton distribution. The consistency of CPR Mark I sampling was also addressed through comparisons with the Plankton Indicator in the North Sea (Hardy & Ennis, 1936).

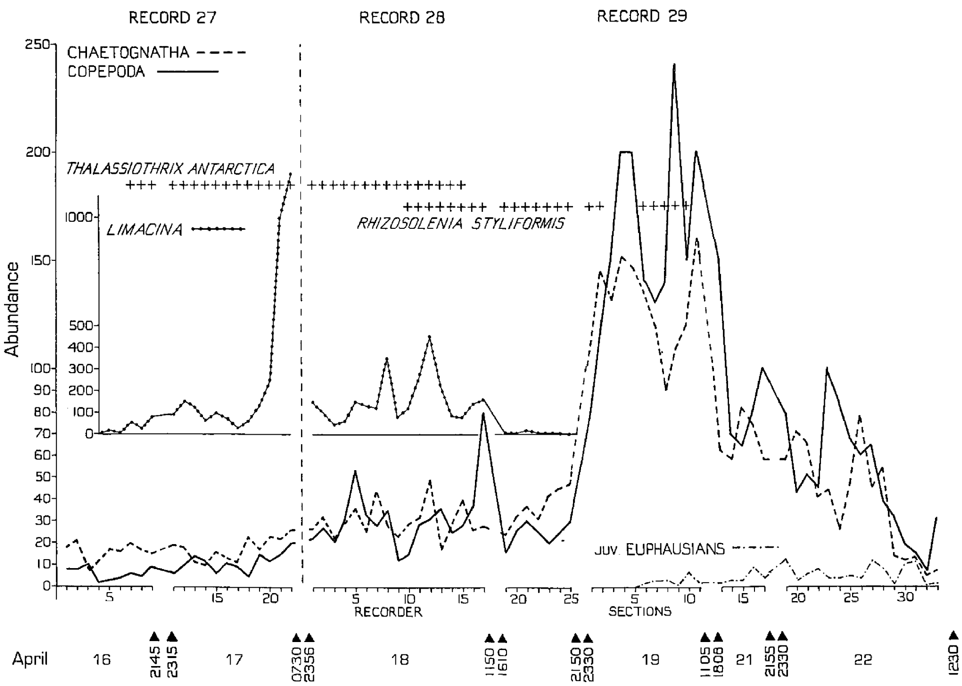


Fig. 6. Abundance of plankton sampled by CPR Type I along a transect across the Drake Passage in April 1926. The presence of the diatoms *Thalassiothrix antarctica* and *Rhizosolenia styliformis* are indicated by crosses. Redrawn after Hardy (1936).

5.3. The Plankton Indicator 1928–1934

When Alister Hardy took up his professorship at Hull University College in 1928 he started to study the relationship between herring and plankton using a Mark II version of the Plankton Indicator. In work completed in 1934 (e.g. Hardy, 1936b) he demonstrated that herring avoided dense blooms of phytoplankton (*Phaeocystis* and large diatoms, such as *Biddulphia*). Also total herring catches in water characterised by high numbers of *Calanus* were double those in water poor in *Calanus*. If statistics are applied to his results the correlation is significant ($P < 0.01$). The Plankton Indicator was then proposed as a tool to help skippers to assess fishing prospects on the basis of the nature and abundance of plankton present.

5.4. CPR pioneer period 1929–1937

In 1929 Hardy designed a Mark II version of the CPR at Hull, which was considerably smaller and hence more suitable for towing behind commercial ships. By the summer of 1931 trial tows were initiated in the North Sea. The results of a 100-mile tow taken in June 1931, before the survey proper was begun in September 1931 and the start of the full operational survey in June 1932, were published by Hardy in 1939. The new CPR was also used in the Southern Ocean on *Discovery II* in 1932 when 9000 nautical miles were towed between stations (John, 1934). Sadly there is no record of the analysis or storage of these samples. The effort that was needed to complete and write up the research with the Plankton Indicator and a decision to publish the results in a new in-house journal delayed the publication of the results of the CPR survey in the 1930s. The first volume of the *Hull Bulletins of Marine Ecology* was published during the war years between 1939 and 1944 and describes the working methods, the design of the CPR, the limitations of the survey, and the interpretation of results for the period 1931 to 1937.

In describing the early results and limitations of the survey, Hardy (1939) focused on the criteria that were used in the selection of a standard depth of 10 m by comparing results with other surveys and demonstrating that 10 m was close to the mid-water depth horizon over much of the North Sea. The effects of stratification and fronts on plankton distribution were not considered, basically because the role of these phenomena in influencing plankton distributions were poorly understood at that time. Vertical migration was also discounted as a factor that might influence counts of copepods when it was shown that results from all tows on the Bremen line in 1932–1934, when aligned as a standardised plot on their midday point, showed no systematic evidence of diurnal variability (Fig. 31 in Hardy, 1939).

The phytoplankton results presented by Lucas (1940) focussed on large diatoms and *Phaeocystis* and were directed towards further testing of the herring-avoidance hypothesis. Considerable patchiness was observed in the phytoplankton results. Even in the 1930s, when eutrophication was not perceived as a problem, extensive blooms of *Phaeocystis* occurred in the southern North Sea, with maximum concentrations along the continental coast as at present (Fig. 7). In the 1930s *Phaeocystis* was quantified by scraping it off the silks and measuring its volume in a tube. For this reason the analysts only recorded it when its presence was clearly evident in the samples. From 1931 to 1937, there was a general increase in plankton numbers, except for *Phaeocystis*. Copepods (Rae & Fraser, 1941) showed great variability in numbers and in relation to North Sea topographic features such as the Dogger Bank. The high summer populations observed in 1935 and 1937 were followed by lower numbers in the subsequent winter. Conversely good winters appeared to be followed by poorer summers, e.g. 1931, 1933 and 1934. It was also noted that high copepod numbers in 1932 and 1937 were followed in the subsequent year by dense spring blooms over the Dogger Bank.

5.5. CPR: A time of change 1937–1939 and 1946–1947

As Hardy (1939) indicated, the pre-war survey was of a pioneering nature, with progressive minor refinement of the CPR design, changing analysis procedures, identification of the limitations of the methods,

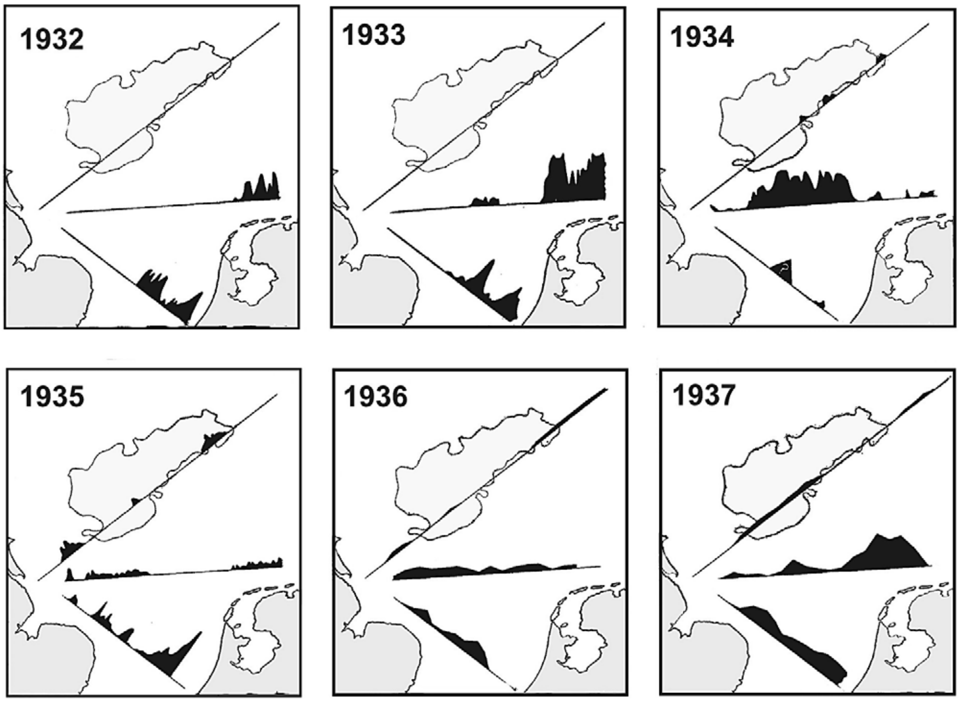


Fig. 7. Abundance of *Phaeocystis* along transects across the southern North Sea between 1932 and 1937 (Redrawn after Lucas, 1940). Dogger Bank outlined in light grey.

refining the geographical focus, and developing the logistical aspects of the work. In January 1938 the survey expanded into the northern North Sea and, in April 1939, into the North Atlantic with the first tow along the V route to Iceland. A second laboratory was opened in Leith Docks, Edinburgh, to service this expansion with Dr C. E. Lucas in charge. The advent of war delayed publication of the results of the survey in the late 1930s. Relevant papers for the period up to 1947 appeared in volumes II and III of the *Hull Bulletins of Marine Ecology*, published between 1941 and 1954. For the first time it became possible to differentiate between 'oceanic' copepod species, such as *Metridia lucens,* species found over the deep trench off Norway such as *Calanus hyperboreus*, central North Sea species such as *Labidocera wollastoni* and south-east species such as *Corycaeus anglicus* (Rae & Rees, 1947). Rees (1949) recognised that two forms of *Calanus*, namely *finmarchicus* and *helgolandicus*, could be distinguished. He showed that their patterns of occurrence were different and that they were introduced into the North Sea from the north-west, but he did not recognise them as different species, as Sars had proposed in 1903.

The size of 38,000 diatom cells was measured in the period 1931–1939 (Lucas & Stubbings, 1948) in a further attempt to distinguish phytoplankton patches, which continued to be a focus of research. It was also demonstrated that *Biddulphia sinensis* varied in size with salinity. An overview of CPR records of young fish and fish eggs for the period 1932 to 1949 was given by Henderson in 1954. Though the numbers caught were low, clear spatial, seasonal and interannual patterns could be demonstrated, and a correlation was observed between numbers of fish eggs in the North Sea and landings of demersal fish per unit effort of fishing.

A gap of 8 years occurred during the Second World War and its aftermath when normal merchant-ship trading ceased. The laboratory in Hull was reopened by Dr Lucas in May 1945, followed in January 1946 by the first post-war deployment of a CPR along a mine-free corridor from Hull to Copenhagen using the

SS *Spero*. This was the same vessel (see Fig. 4) that had initiated the operational survey in June 1932 and had survived the war. When the survey restarted after the war, a set of procedures was established that has remained virtually unchanged ever since (see Methods above). Any changes introduced were made with strict regard to the consistency of the final data. This has been a paramount concern throughout the history of the survey.

When the new post-war survey started in 1946 the sampling coverage soon expanded out into the Atlantic and many of the problems of the pioneer years had to be addressed once again, such as what research to do during the first few years until data had accumulated. The main tasks of the early years were the development of streamlined procedures for processing silks and analysing samples. These processes are labour-intensive and a compromise was reached by developing a routine analysis for the most common taxa and by only analysing every alternate block (Rae, 1952).

5.6. Post-war Indicator Survey 1947–1976

After the Second World War, a new Indicator Survey was established over a 12-week summer period in the north-western North Sea (Glover, 1957). This was a continuation of the pre-war studies by Hardy aimed at “establishing whether or not the movements and aggregations of herring were influenced by the quantity and composition of the plankton” (Bainbridge & Forsyth, 1972). Between 1947 and 1974 there were substantial changes in the plankton, most notably ca. 1951/2 and 1958/9 when the communities switched from being a neritic to a northern intermediate shelf fauna and back again (Bainbridge & Forsyth, 1972; Williamson, 1961). After 1959 *Calanus finmarchicus* and *Spiratella retroversa*, characteristic species of the northern intermediate fauna and key food items of the herring, showed pronounced reductions in numbers until 1974 throughout the north-western North Sea. The timing of this change coincided with a northerly movement of the herring stocks from the Buchan to the Shetland area at the time of the autumn fishery, followed later by declining stocks (attributed to overfishing) in the Shetland fishery. Statistical analyses by Williamson (1961) on this set of data demonstrated the importance of the stability of the water column for the spring growth of phytoplankton and the subsequent composition of the summer zooplankton. As new fishing methods were introduced, the size of the drifter fleet rapidly declined and with it the number of samples taken; in consequence, the Indicator Survey was closed down in 1976.

5.7. Shape of distributions 1948–1957

In 1948, Mr. K. M. Rae succeeded as head of the survey and oversaw the transfer in April 1950 of the whole organisation from the University College of Hull to a laboratory in Leith under the auspices of the Scottish Marine Biological Association (SMBA). At the same time the in-house journal, the *Hull Bulletins of Marine Ecology* changed its name to the *Bulletins of Marine Ecology*. From this period annual reports of the status of the plankton in the areas sampled by the CPR were regularly published in the journal *Annales Biologiques* (e.g. Glover & Robinson, 1972) until the journal ceased publication in 1984. In October 1952 the Oceanographic Laboratory, Edinburgh, was opened as the base for the survey, followed in 1957 by the appointment of Mr. R. S. Glover as officer-in-charge.

Prior to the development of the CPR survey most distributional maps of marine plankton were based on the results of expeditions, one-off surveys or collaborative international programmes, such as the 1902–1908 surveys by ICES (Le Bureau du Conseil & Kyle, 1910; Rozwadowski, 2002). A drawback to their mapped products was the irregularity in time and space of the observations and the very variable sampling equipment used, so geographical gradients in abundance could not be determined. With the introduction of ocean weatherships CPR routes were extended into the Atlantic in 1947, thus allowing the seasonal and interannual patterns of plankton abundance and distribution to be studied on an ocean-basin scale over many years. To demonstrate biogeographic patterns, results based on 15,171 samples and 65 taxa were synthesised for the 9-year period 1948–1956 to produce the first Plankton Atlas. This atlas was issued in a series of parts (e.g. phytoplankton, Robinson, 1965; Thaliacea, Hunt, 1968) in volume V onward of the *Bulletins of Marine Ecology*. To summarise the data, mean results were averaged for the first time into ICES statistical rectangles of 1° latitude by 2° longitude. All the processing of close to a million data items was done manually, using pencil and paper and electro-mechanical calculators, so the final products were the result of many months of toil. The species studied in the atlas project were categorised as oceanic, intermediate, neritic and unclassified (Fig. 8) on the basis of their 'average' biogeographic patterns (Colebrook, Glover, & Robinson, 1961).

A particular feature of research published during this period was the detailed studies on planktonic larval stages. Rees (1950) identified more than 50 taxa of bivalve larvae. He demonstrated that the numbers of pelagic larvae did not reflect the abundance of adults in the benthos, but were highest over cohesive sediments (Rees, 1951). He also demonstrated that the larvae could be transported considerable distances from their source (Fig. 2 in Rees, 1951). Similar studies were also completed for decapods (Rees, 1952) and for young fish and eggs (Henderson, 1954).

In a series of papers, e.g. Bary (1964), plankton distributions in 1957 were related to the distribution of water masses in the Northeast Atlantic and coastal waters of the British Isles by comparing plankton results with sea-surface temperature and salinity averaged for ICES rectangles of 1° latitude × 2° longitude. At this time the thinking in plankton ecology linked the distribution of species to water masses, the major current systems, and to local topography. This was the age of the 'Indicator Species'.

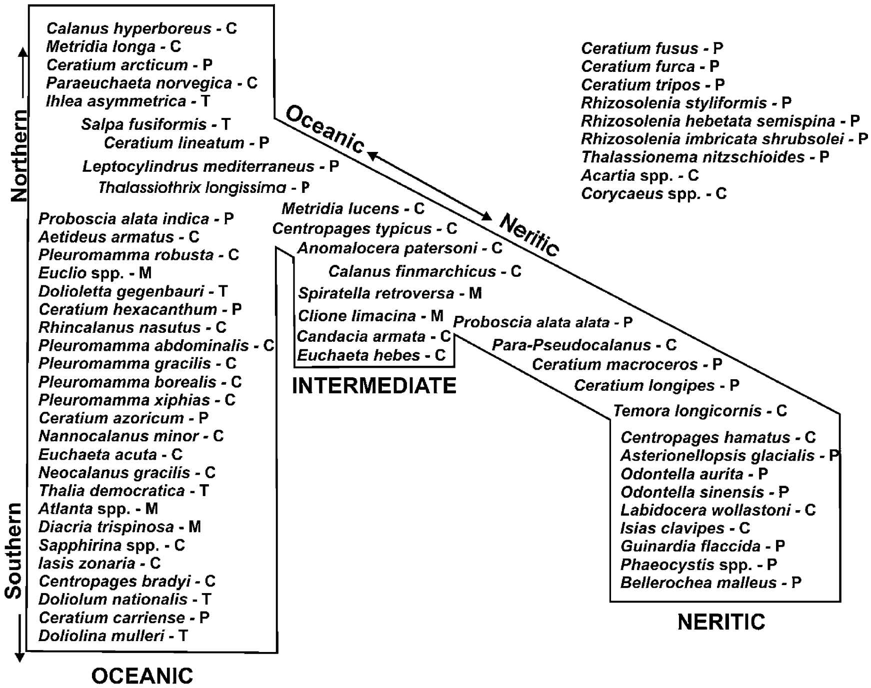


Fig. 8. Classification of plankton (taxonomy updated) into Neritic, Oceanic and Intermediate distributions after Colebrook, Glover and Robinson (1961).

5.8. Expansion to the western Atlantic 1958–1968

The year 1958 signalled the start of a new standardisation of all analytical procedures (Colebrook, 1960). The expansion of the survey into the western Atlantic was made possible with funding from the USA Office of Naval Research. Results from the 11-year period 1958–1968 were used to compile a new CPR Atlas with mean distributions for 255 taxa (Edinburgh Oceanographic Laboratory, 1973). Specialist studies were completed on specific groups, e.g. tintinnids (Zeitzschel, 1965) and Cladocera (Gieskes, 1971). Studies of fish larvae helped to define more precisely the extent and variability of newly discovered stocks of *Sebastes* in the Irminger Sea (Henderson, 1961; Bainbridge & Cooper, 1971) and blue whiting over deep water to the west of the United Kingdom (Henderson, 1957; Bainbridge & Cooper, 1973).

At this time most CPR analysts were also experts in particular taxonomic groups and undertook specialist analysis of these groups after the routine analysis was completed. *Calanus* provides a particularly interesting example. Sars (1903) had recognised two closely related species, *C. finmarchicus* and *C. helgolandicus*, but many subsequent copepod specialists considered them to be a single species. The first person seriously to suggest that *C. helgolandicus* should be re-instated as a 'true' species, was Rees (1949) working on CPR samples; thereafter they were distinguished when possible in routine CPR analyses (Rees, 1957), but not recorded in the database until 1958. By the mid 1960s, Matthews (1967) was able to chart the complementary distributions of the two forms, by then generally accepted to be distinct species, and hence to contribute to the wider debate on the degree of speciation within the *C. finmarchicus* complex. A third species, *C. glacialis*, had been described by Jaschnov (1957) from the Atlantic sector of the Arctic, but the morphological distinction was very fine and it seemed quite likely that the two were forms that differed only in size and size-related morphometrical features, along a scale that could be related to temperature. Experiments conducted by Matthews (1966) supported this view and it was hypothesised that the apparent bimodality in size and form was the result of the smaller area of subarctic Atlantic compared with the Arctic—where '*C. glacialis*' is endemic—and of the cold-temperate Atlantic—where *C. finmarchicus sensu stricto* is to be found. Although subsequent studies have not supported this view, the CPR samples have provided a unique record of the process of speciation that has been followed by the creature that is arguably the most successful and ubiquitous of oceanic plankton.

Off the east coast of England the Fisheries Laboratory at Lowestoft had sampled a series of stations called the 'Flamborough Line' in a transect running NNE into the North Sea between 1932 and 1961. Colebrook (1966) demonstrated that the interannual variations in the plankton from these stations were more closely correlated with variations in a group of CPR ($2° \times 1°$) rectangles in the northern North Sea than in rectangles off the Humber immediately to the south. This result pre-dated the definition of the Flamborough Front (Pingree & Griffiths, 1978) and established that there were well-defined hydrographic boundaries between water masses in the North Sea.

Colebrook (1963) showed that the statistical rectangles used in the earlier atlas study could be grouped together into larger 'standard areas'. In later years many studies made use of this coarser geographical division to examine seasonal and interannual variability over the whole of the northern North Atlantic. By averaging results into these larger areas it was demonstrated that marked changes in seasonal and interannual patterns of abundance, timing and season duration occurred and that the patterns of change frequently differed between the North Sea and eastern Atlantic (Colebrook, 1965; Colebrook & Robinson, 1964; Glover, 1967). For example, the diatom *Thalassiothrix longissima* and the copepod *Corycaeus anglicus* showed alternating years of abundance in the North Sea, and the gastropod, *Spiratella,* showed a marked reduction in numbers after a period as a common member of the plankton in the eastern Atlantic, but remained common in the North Sea. It was also demonstrated that the timing of the spring bloom was similar to the pattern of temperature difference (Craig, 1960) and thus the development of stratification between different regions of the Atlantic (Fig. 9).

Computers were introduced to the survey during this period and Colebrook (1964) published the first

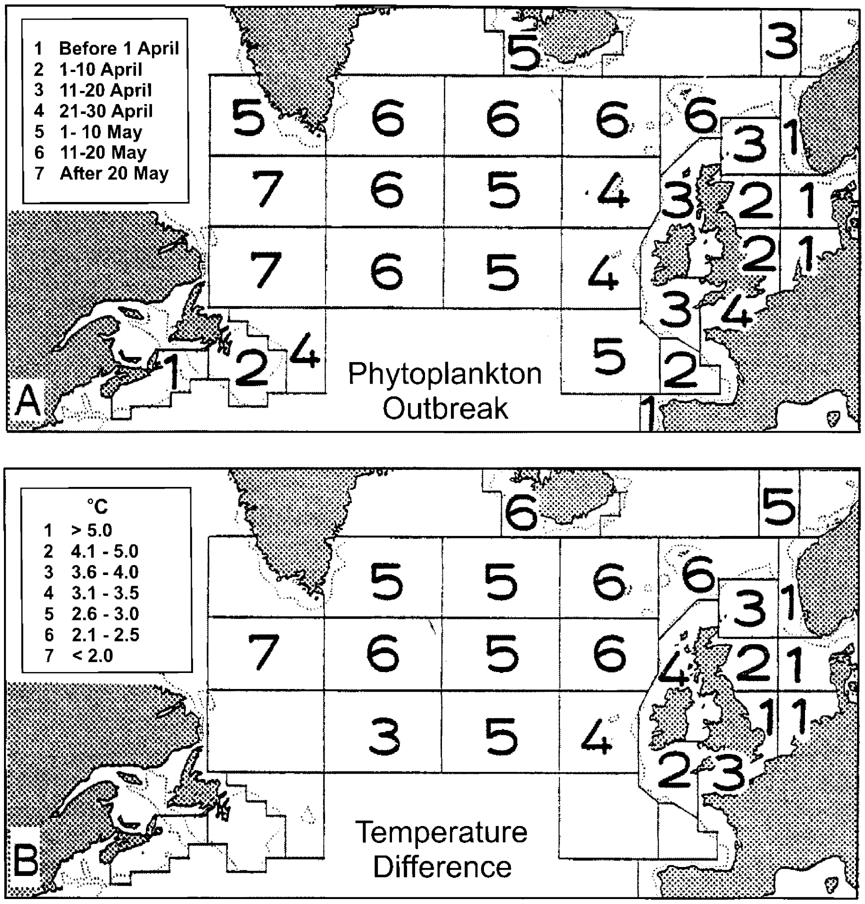


Fig. 9. Maps indicating the timing of the first seasonal bloom of phytoplankton and temperature difference averaged for CPR Standard Areas (from Glover, 1967).

of many papers that used principal component analysis (PCA) to investigate variability. This analysis, based on the same data used to produce Fig. 8, allowed five clear distribution patterns to be distinguished (Fig. 10). The calculations were completed on a basic matrix processing programme using a DEUCE computer at the University of Glasgow. Most of the species included in the analyses, with some exceptions such as the Southern Intermediate distribution, could be classified along an oceanic/neritic axis.

The generally perceived view of the relationship of zooplankton to phytoplankton at this time was that more phytoplankton should mean more zooplankton. Colebrook and Robinson (1965) examined geographical variations in the seasonal cycle of gross estimates of phytoplankton and zooplankton, average abundance, timing (early or late) and season duration (the length of the productive period). The correlations between these variables showed that the abundance of zooplankton was correlated with timing and season duration, but not with the abundance of the phytoplankton (see also Colebrook, 1979). Distributions were similar in the early and late months of the year in contrast to marked differences in the summer months. Furthermore, the geographical pattern of early timing and long season looked similar to the second principal component in the atlas data, thus establishing a link between geographical and seasonal patterns. Robinson (1970) used PCA to investigate the seasonal cycles of phytoplankton in the North Atlantic and showed that

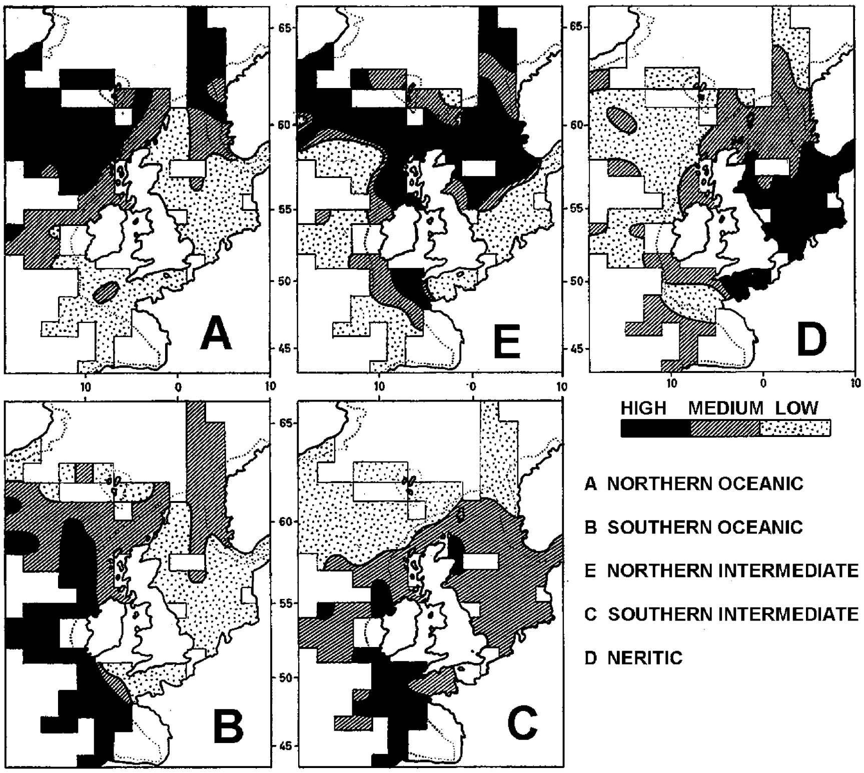


Fig. 10. Classification of plankton on the basis of principal component analysis into five geographical distribution types. Redrawn from Colebrook (1964).

the variation in the observed patterns was in part related to the development of stratification, as measured by the rate of increase of temperature.

During the 1960s trials were initiated in the freshwater ecosystems of the Great Lakes to determine the feasibility of establishing a ship of opportunity CPR programme (Robertson, 1968 and personal communication). The summer crustacean zooplankton communities sampled in Lakes Erie and Ontario were found to be more diverse and to have greater numbers of zooplankton per cubic meter than in equivalent samples from the North Atlantic (Table 1). Preliminary results indicated that the plankton from Lakes Huron and Michigan were less abundant than in the marine environment. As the majority of freshwater crustaceans were smaller than their marine equivalent trials suggested that a finer silk mesh (82 meshes per inch compared to the 60 mesh used by the CPR survey) should be used in freshwater systems. Some of the machines were modified by increasing the size of the front aperture to take account of the lower densities of plankton.

5.9. Peak years and computerisation 1968–1976

A flowering of the survey took place at the Oceanographic Laboratory, Edinburgh from 1968 to the early 1970s with the maximum route extension and experimental tows in other regional seas outside the core area of the North Atlantic, e.g. pilot tows in the Gulf of Mexico. Mr G. A. Robinson succeeded as officer-in-charge in 1970. A strong instrumentation group was established in the laboratory, which led to the development of the Undulating Oceanographic Recorder (Bruce & Aiken, 1975) and its successors.

Table 1
The mean number of species of microcrustacea and total number of zooplankton species per CPR sample and the mean abundance of microcrustacea and total zooplankton per CPR sample, as individuals per m^3, averaged for a range of environments along a west to east series of CPR tows from Lake Erie to the Grand Banks in July/August 1966

Environment	Species of micro-crustacea	Total species of zooplankton	Abundance of micro-crustacea	Total abundance of zooplankton
Lake Erie	9.5	9.5	8295	8295
Lake Ontario	4.9	4.9	259	259
St. Lawrence Estuary	1.2	1.4	20	20
Gulf of St. Lawrence	1.9	3.4	111	113
South of Newfoundland	2.1	3.1	67	92
Grand Banks	1.7	3.8	35	139
East of Grand Banks	1	1.9	25	31

Electronic logging instruments were also attached to CPRs for the first time (Aiken, Bruce, & Lindley, 1977; Aiken, 1980).

Manual data processing and plotting of results on maps took up much of the time of the analysis team until 1969 when computerisation was first introduced; this was fully implemented in 1971 (Colebrook, 1975; Stevens & Reid, in press). Principal component analysis applied to the data from 12 standard areas in the Northeast Atlantic (Colebrook, 1978) confirmed the downward trend in the abundance of many zooplankton taxa first identified by Colebrook (1972a,b) and Glover, Robinson and Colebrook (1972). A major achievement during this time was the publication of the first comprehensive CPR atlas, which has remained a key reference source until the present day (Edinburgh Oceanographic Laboratory, 1973). A number of specialist supplements came later, e.g. fish larvae (Coombs, 1980), tintinnids (Lindley, 1975) and ostracods (Williams, 1975). On the basis of the results presented in the atlas (Colebrook, 1972b) refined his distribution types into seven categories (Neritic, Northeast Intermediate, Northeast Oceanic, Southeast Intermediate, Southern Oceanic, Western Intermediate and Northwest Oceanic), which matched the known current systems of the North Atlantic (Fig. 11). Scanning electron microscope studies of the reproductive

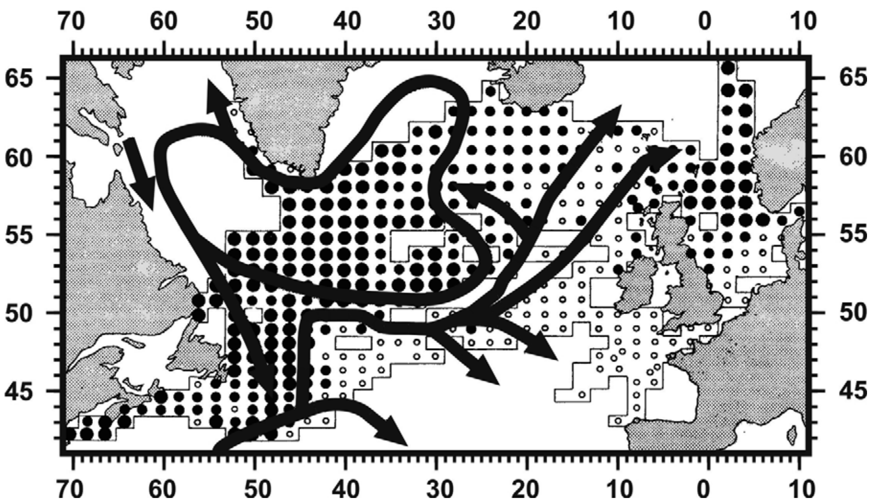


Fig. 11. Map of the occurrence and abundance of *C. finmarchicus* V–VI averaged for statistical rectangles as per the 1973 CPR Atlas with superimposed the main circulation of the northern Atlantic. Redrawn from Colebrook (1972b).

structures of the Centropagidae (Lee, 1972) were undertaken as part of a PhD study into the population structure of two copepod species from CPR material by Lee (1971).

From 1971 to June 1975 in the months of March to October an ecological study of the vertical distribution of plankton using the Longhurst Hardy Plankton Recorder (LHPR) was run from Ocean Weather Ships at Stations *India* and *Juliet* in the eastern Atlantic by Mr. R. Williams from the Oceanographic Laboratory in Edinburgh (Williams, 1988). The LHPR is a vertical profiling system that samples plankton in a similar way to the CPR (Longhurst & Williams, 1976). The OWS ships towed CPRs while en route to or from the weather station, and the vertical sampling programme was undertaken in the weeks between their arrival and departure from station. This timing enabled the results from many vertical plankton profiles to be placed in the context of the CPR survey (e.g. Williams & Robins, 1981; Williams & Lindley, 1982). After June 1975 an intermediate weather station (*Lima*) replaced *India* and *Juliet*, which reduced CPR coverage of the eastern Atlantic. The OWS programme at Station *Lima* was finally closed down and the last CPR towed when OWS *Cumulus* returned to the Clyde in May 1996.

Large-scale changes in the phytoplankton of the North Sea and Northeast Atlantic, which involved an apparent inversion of diatom to flagellate abundance over the period 1958 to 1973 (Fig. 12), were described by Reid, 1975, 1978a), and fluctuations in larval fish abundance by Coombs (1975). Gieskes and Kraay (1977) compared averaged results from a small coastal area under the influence of the Rhine against the wider North Sea. Annual changes differed between phytoplankton and zooplankton, but were similar between the nearshore and offshore areas. Data for Phytoplankton Colour showed more marked increases in coastal waters than elsewhere. However, corresponding results for diatoms and dinoflagellates did not totally explain the phytoplankton colour changes; the difference was attributed to an increase in microflagellates and other unidentified species that disintegrate in formalin. The changes were considered as a possible response to eutrophication. Gieskes and Kraay (1977) also showed that the concentration of all chlorophyll derivatives measured in their analyses was correlated with the colour index, reinforcing the view that the index can be used as a proxy for phytoplankton biomass.

This period came to an end with the closure of the Oceanographic Laboratory in Edinburgh and the transfer of staff and equipment to a new operational home for the survey at IMER (later to become the Plymouth Marine Laboratory) in Plymouth, England. It was unfortunate that this transfer in 1976 took

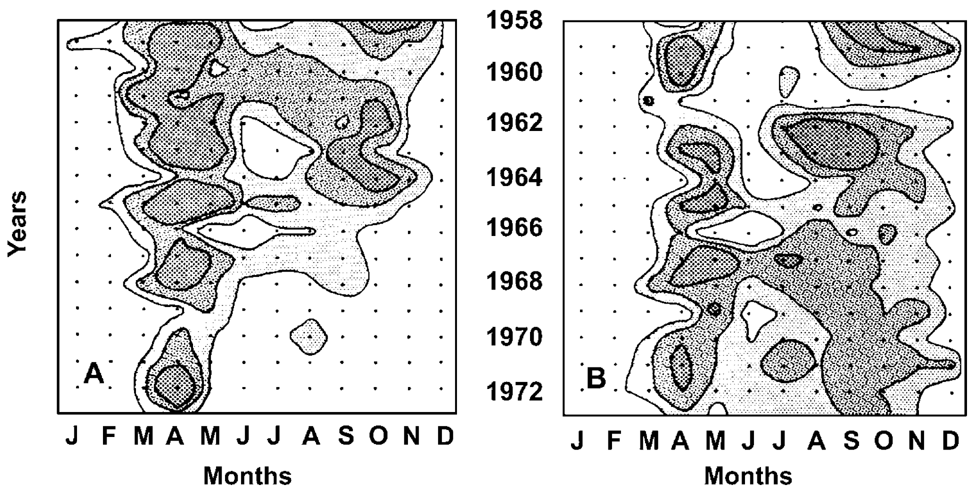


Fig. 12. Isopleth diagram of the monthly abundance of (A) diatoms and (B) Phytoplankton Colour (visual chlorophyll) for the years 1958 to 1972 showing the inverse pattern seen between the two indices. Increasing depth of greyness equals higher abundance or colour intensity. Redrawn from Reid (1975).

place at a time when a major international study of the spring bloom, the Fladen Ground Experiment (FLEX 76), was taking place in the northern North Sea. The results from the CPR survey gave important background to FLEX (e.g. Lindley & Williams, 1980; Williams & Lindley, 1980), but many of the CPR tows planned to coincide with the research-vessel programme failed, almost certainly because of the change in technical personnel.

5.10. Plymouth period 1977–1988

Against this background of a change in the location of the home laboratory, the research productivity of the CPR survey remained high, with the publication of a number of what are now seen as classic ecological papers. With improved computing facilities, Colebrook and others produced a series of papers on the CPR, beginning in 1978 with 'Zooplankton and Environment 1948–75' in volume 1 of Oceanologica Acta (Colebrook, 1978, 1979, 1981, 1982a,b,c, 1985a,b, 1986a,b, 1991; Colebrook & Taylor, 1984; Colebrook, Reid, & Coombs, 1978). Colebrook's papers examined long-term changes (1978), geographical patterns, the amplitude, duration and timing of seasonal cycles (1979), succession and persistence (1981, 1982a,c), overwintering (1985a), population dynamics (1982b), sea-surface temperature (1985b), shelf-edge boundaries (1986a) as well as the environmental forcing (1982c, 1986b) behind observed changes in plankton such as the effect of wind speed and direction on phytoplankton growth (see Dickson & Reid, 1983; Dickson, Kelly, Colebrook, Wooster, & Cushing, 1988).

Colebrook (1979) repeated the analysis of geographical variability in the seasonal cycles of phytoplankton and zooplankton published in 1965 for a much wider geographical area, confirming his earlier results and drawing attention to an apparent surplus of phytoplankton in the open ocean in the summer. In an examination of seasonal cycles of geographical distribution, Colebrook (1984) contrasted three abundant species of phytoplankton that exhibited similar, extensive seasonal changes in distribution with *Pseudocalanus*. The average seasonal cycle for three diatoms and for *Pseudocalanus*, presented in vector space, is shown in Fig. 13. The sensible strategy for a grazing species of zooplankton would seem to be to track the seasonal changes in distribution of the phytoplankton. This did not happen in this case as *Pseudocalanus* showed a much more restricted seasonal range in distribution than the phytoplankton species. The inference is that a low reproductive rate compared with that of phytoplankton prevents *Pseudocalanus* from exploiting the seasonal range of the phytoplankton. It follows that the distribution of *Pseudocalanus* throughout the whole season is constrained by the areas where it can survive the winter most successfully. This finding indicated that the plankton ecosystem, at least in the Northeast Atlantic, is not a finely tuned and balanced system geared towards the efficient exploitation of the phytoplankton. This conclusion is highly relevant to the role of the ocean as a carbon sink. Colebrook (1982b) confirmed (Fig. 14) that a significant proportion of the spring bloom of phytoplankton between about 45° and 60°N is not grazed. There are insufficient zooplankton species over-wintering in the area and capable of reproducing fast enough to fully exploit the phytoplankton spring bloom. The 'surplus' phytoplankton is a potential carbon sink. It was subsequently confirmed that much of the spring bloom does sink and reach the deep ocean floor (Billet, Lampitt, Rice, & Mantoura, 1983, see also Lampitt & Antia, 1997).

During this period Colebrook and other colleagues noted (Fig. 15) that the general downward trend that had occurred in the zooplankton since the survey restarted after the war and in the phytoplankton since ~1960 (Colebrook, 1982c) appeared to have reversed (Colebrook, Robinson, Hunt, Roskell, John, Bottrell et al., 1984). The trend was later related to westerly weather and shown to include a 3-year cycle (Colebrook, 1986b). It was suggested that the long-term trend was established in winter through an effect on over-wintering stocks while the 3-year pattern was established later in the year. An update of the trend has been published by Reid and Hunt (1998). Colebrook (1991) speculated that the overall dynamics of the pelagic seasonal cycle is determined by the zooplankton and that, apart from the spring bloom, phytoplankton populations are determined by in situ recycling of nutrients from the zooplankton.

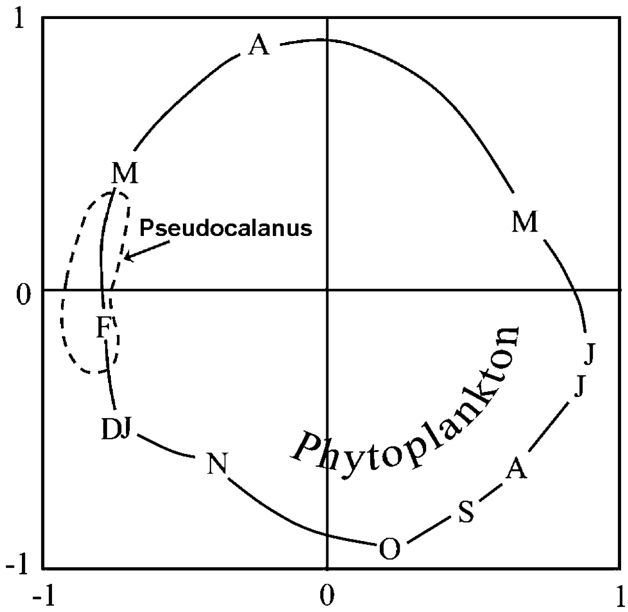


Fig. 13. One example of a vector plot from Fig. 5 (Colebrook, 1984) showing the difference in the variation of the seasonal distribution of *Pseudocalanus* spp. against the same pattern for a group of diatoms. The vectors for each month of the phytoplankton group are joined by a continuous line and for *Pseudocalanus* by a dashed line.

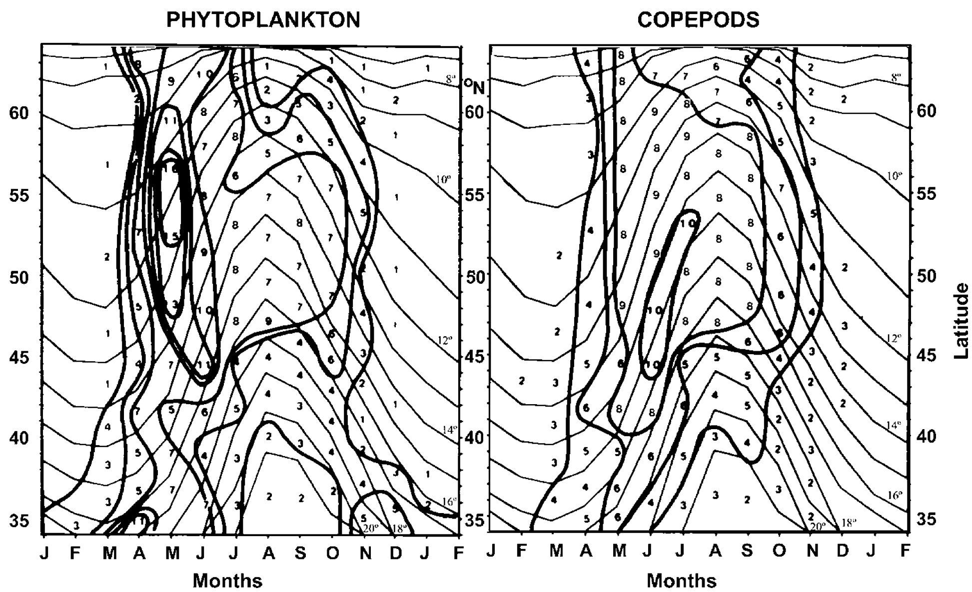


Fig. 14. Month–latitude diagrams for the northern Atlantic showing isotherms at 1 °C intervals with superimposed contours of the intensity of phytoplankton colour and abundance of total copepods. Redrawn from Colebrook (1982b).

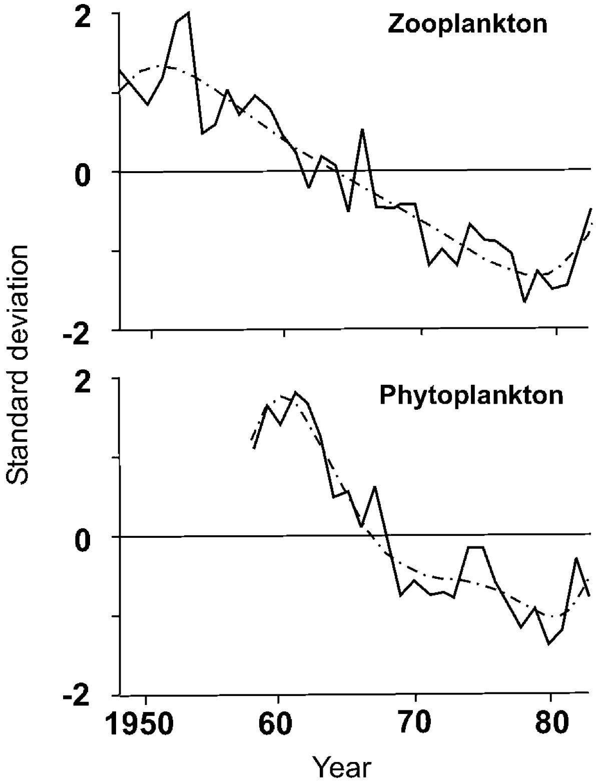


Fig. 15. Long-term trends in the annual fluctuations of zooplankton (1948–1983) and phytoplankton (1958–1983) averaged for the eastern North Atlantic, Atlantic shelf around the UK and North Sea. The graphs, plotted as standardised (zero mean, unit standard deviation) time series, are first principal components with a smoothed fifth-order polynomial superimposed. Redrawn after Colebrook et al. (1984).

Also at this time Lindley studied the ecology, population dynamics and production of euphausiids in a series of papers (e.g. Lindley, 1977, 1982), followed by similar studies on decapods (e.g. Lindley, 1987, 1988). Reid (1978b) and Reid and John (1978) described resting cysts of dinoflagellates and tintinnids, respectively. Reid (1984) linked CPR data to fisheries statistics for the first time, and Reid, Robinson and Hunt (1987) studied the seasonal evolution of phytoplankton blooms. Marked long-term changes in the abundance of *Phaeocystis* spp., nuisance algae that form dense blooms in the southern North Sea, were described by Owens, Cook, Colebrook, Hunt and Reid (1989). The downward trend seen in the offshore waters sampled by the CPR appeared to be the reverse of the pattern seen in the shallow, eutrophic waters off the continental coast. The spread of a new large diatom, *Coscinodiscus wailesii*, which had apparently been introduced to UK waters, was observed by Robinson, Budd, John and Reid (1980).

This period of scientific productivity was sadly brought to a premature end when notice of the closure of the survey was announced by NERC in July 1988. In the early 1980s monitoring was considered to be weak science, akin to stamp collecting, and process-based research, laboratory experimentation and modelling came to the fore in the United Kingdom. The survey was run down, as evident from the mileage towed (Fig. 1); by November 1986 (when the Z route was stopped) the survey had contracted to 20°W in the eastern Atlantic and the staff had reduced to eight. During the period from 1986 until the closure in March 1989, Mr. R. Williams took over responsibility as head of the survey within PML and continued to co-operate with the survey after its closure. Dr. Colebrook and six colleagues were made redundant on

Friday 31 March 1989 and the survey ceased to operate as part of Plymouth Marine Laboratory and the UK Natural Environment Research Council.

Just 4 years previously, on 22 May 1985, Sir Alister Hardy died peacefully in hospital, aged 89.

5.11. Revival and recent times 1989–2002

The news of the impending closure of the CPR survey in 1988 was followed by an international campaign to ensure its survival, strongly supported by the International Council for the Exploration of the Sea (ICES) and the Intergovernmental Oceanographic Commission (IOC) communities. The staff of the survey returned to work the Monday after closure, on a part-time basis, funded through a rescue package put together by the UK Ministry of Agriculture, Fisheries and Food (MAFF). A skeleton survey was maintained until a new charitable foundation, the Sir Alister Hardy Foundation for Ocean Science (SAHFOS), was established in 1990 to operate the survey into the future. Dr. J. M. Colebrook took over temporarily as team leader until Dr. J. Gamble was appointed as the first Director of SAHFOS in 1991. He was succeeded by Dr. P. C. Reid in 1994. The foundation started to operate formally in April 1991 with international funding from four countries (Canada, Iceland, UK, USA), the European Commission and IOC, after an international fund-raising campaign led by Dr. R. R. Dickson of MAFF. Dr. M. Whitfield, Director of the UK Marine Biological Association, also played a key role in the establishment of the new foundation.

New appointments were made and with them came new approaches to the interpretation of the CPR data and a more detailed analysis of the consistency of the data. From 1991 onwards, annual reports of the work of SAHFOS have been produced and readers are referred to these for additional information. Results from the survey formed an integral part of the reviews of North Sea phytoplankton by Reid, Lancelot, Gieskes, Hagmeier and Weichart (1990) and North Sea zooplankton by Fransz, Colebrook, Gamble and Krause (1991).

A key publication at the beginning of this period was the paper in *Nature* by Aebischer, Coulson and Colebrook (1990) which demonstrated that the long-term trend in zooplankton and phytoplankton in CPR data, as defined by the first principal component of an analysis of long-term change, was coincident with westerly weather, herring landings and three measures of the breeding performance of kittiwakes in the north-western North Sea (Fig. 16). This work was followed by a publication authored by 'The CPR Survey Team' (1992), which suggested for the first time that the commonality of trends and the changes seen in the late 1980s could be linked to climate change and global warming. Gamble (1994) developed this theme, further placing some case histories from the CPR in the context of marine environmental change. Reid and Hunt (1998) updated the PCA analyses and further developed the apparent linkage with climate change.

New themes addressed included descriptions of unusual events in the plankton (Dickson, Colebrook, & Svendsen, 1992; Lindley, Roskell, Warner, Halliday, Hunt, John et al., 1990; Edwards, John, Hunt, & Lindley, 1999), studies of copepod resting eggs (Lindley, 1997; Lindley & Hunt, 1989), incursion of oceanic diatoms into the North Sea (Reid, Surey-Gent, Hunt, & Durrant, 1992), spread of a non-indigenous diatom on the Northwest European shelf (Edwards, John, Johns, & Reid, 2001), zooplankton year-class strengths (Rothschild, 1998) and copepods and temperature (Lindley & Reid, 2002).

Cushing (1984) attributed the explosion in the recruitment of gadoid fish in the North Sea, known as the 'gadoid outburst', to changes in the occurrence and timing of high numbers of *Calanus finmarchicus* measured by the CPR as an extension of his match–mismatch hypothesis (Cushing, 1990). Brander (1992) re-examined this relationship for cod, concluding that Cushing's multiple regression model does not work because the available data have neither the right detail nor coverage, and the model ignores spatial heterogeneity. Other work by Cushing that has utilised data from the CPR is documented by Corten & Lindley (this volume). Possible fish/plankton interactions attributed to top-down control were examined by Reid, Battle, Batten and Brander (2000) and developed further by Lindley, Reid and Brander (2003) who found an inverse relationship between cod (*Gadus morhua*) recruitment in the North Sea and counts of young

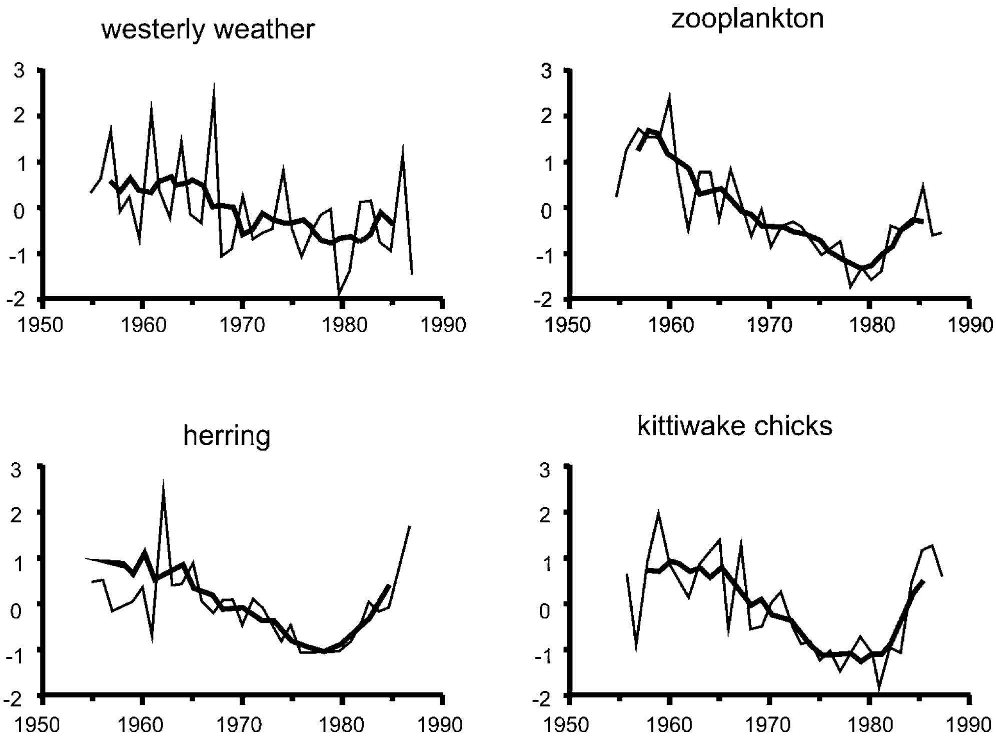


Fig. 16. Parallel trends (1955–1987) in the frequency of westerly weather, zooplankton, herring and kittiwake chicks in the North Sea plotted as standardised time series with superimposed a 5-year running mean. Redrawn after Aebischer et al. (1990).

fish in CPR samples. Parallel trends between CPR data and fishery catches for the basking shark (*Cetorhinus maximus*) from the west of Ireland were used by Sims and Reid (2002) to propose that a declining trend in the stock was a result of a distributional shift in the population rather than to fishery-induced over-exploitation. Further examples of fish/CPR plankton studies are outlined by Corten & Lindley (this volume).

Comparisons between benthic abundance and biomass time series and CPR data from both sides of the North Sea, off the Northumberland coast and in the Skagerrak, have shown a broad coupling in their patterns of change (Austen, Buchanan, Hunt, Josefson, & Kendall, 1991; Buchanan, 1993; Clark & Frid, 2001). Clark (2000) and Clark, Frid and Batten (2001) also compared a zooplankton time series derived from 50 m vertical hauls with a WP2 net off Northumberland with CPR data from adjacent waters. The relative year-to-year fluctuations between the datasets were significantly correlated ($r = 0.64$, $P < 0.001$), although there were large differences in the relative abundances of zooplankton between the two series, which were attributed on the basis of modelling to avoidance of the CPR.

In a series of papers Hays and colleagues investigated patterns of diel vertical migration (DVM) using differences in the day/night occurrence of plankton sampled by the CPR (e.g. Hays, 1996; Hays, Proctor, John, & Warner, 1994). Copepods display considerable spatial variability in DVM, with larger species showing the strongest signals (Hays, Proctor, John & Warner, 1994), so that DVM is more marked in the Northwest Atlantic where larger species predominate (Hays, 1995a, 1996). It was also demonstrated that the length of time spent by copepods near the surface can vary seasonally in a systematic way (Fig. 17) related to day length and thus latitude (Hays, Warner, & Proctor, 1995; Hays, 1995b). Hays (1995c) and Hays, Warner and Lefevre (1996) developed the hypothesis that DVM is a mechanism for predator avoidance by showing a statistical relationship between trends in the biomass of herring spawning stock and

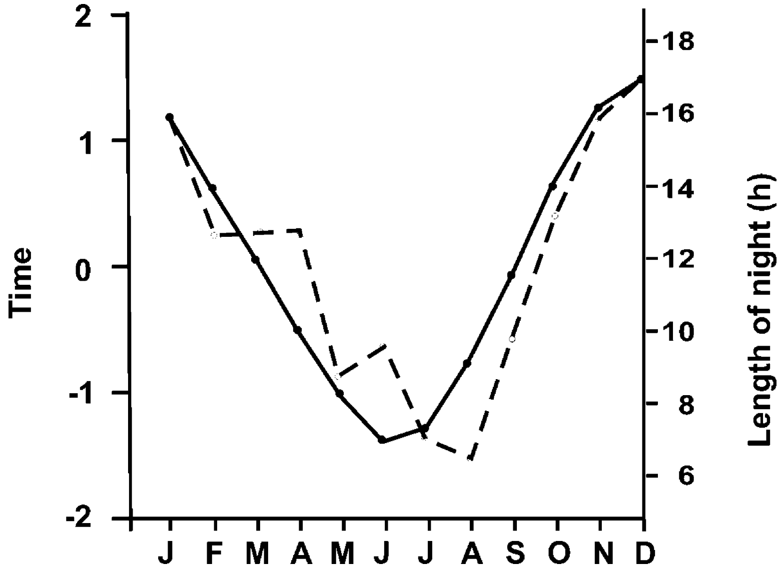


Fig. 17. Mean length of time that *Metridia lucens* was present near the surface in each month (dashed line) and mean length of night in each month (continuous line) both standardised to zero mean and unit variance. The secondary y axis gives the number of hours per night that *M. lucens* was present near the surface scaled to the standardised data. Copepod results based on 34,099 samples from the Northeast Atlantic in the period 1948–1992. There was a significant linear relationship between the two datasets (r^2 = 0.8, $P < 0.001$). Redrawn from Hays, Warner and Proctor (1995).

DVM in *C. finmarchicus* in the North Sea. Hirst and Batten (1998) have reviewed this hypothesis and demonstrated that their results are based on an unsuitable test and therefore unfounded. Using a completely different statistical approach, Beare & McKenzie (1999a) also failed to concur with the thesis of Hays and colleagues that the DVM behaviour of *C. finmarchicus* was statistically dependent on the long-term trend.

A number of studies have been carried out on the sampling characteristics of the CPR and the consistency of the database. This work is covered in more detail in Batten, Clark, Flinkman, Hays, John, John et al., (this volume). Beare & McKenzie (1999b) highlighted problems of sampling coverage and drew attention to aspects of the database that make statistical analysis difficult, as well as outlining a new statistical modelling approach for application to the data. Despite the size of the CPR database, its data have seldom so far been used in modelling studies (e.g. Broekhuizen, Heath, Hay, & Gurney, 1995; Stephens, Jordan, Taylor, & Proctor, 1998; Heath, Backhaus, Richardson, McKenzie, Slagstad, Beare et al., 1999). In the study by Stephens, Jordan, Taylor and Proctor (1998), the authors demonstrated that half the variance of interannual changes in the abundance of *C. finmarchicus* in the North Sea could be attributed to winter inflow from the Atlantic.

Rigorous new statistical analyses of CPR data were applied by Broekhuizen and McKenzie (1995) to distinguish between seasonal patterns, long-term trends and other variability in time series. They concluded that stochastic events rather than advection influenced zooplankton dynamics over large areas with similar hydrographic conditions. In a series of papers Beare and colleagues used statistical models to develop this approach, further demonstrating changing seasonality in *Calanus* species over long periods of time (e.g. Beare & McKenzie, 1999c). This last work and other studies have formed part of large interdisciplinary projects (Investigation of *Calanus finmarchicus* migrations between Oceanic and Shelf seas off Northwest Europe (ICOS), Trans-Atlantic Study of *Calanus finmarchicus* (TASC), and NERC's Marine Productivity Programme) that are examining the mechanisms behind large-scale changes in the population dynamics of *C. finmarchicus* in the North Atlantic. Heath et al. (1999) summarised results from the TASC project and showed that the main invasion route of *C. finmarchicus* into the North Sea is not via the Fair Isle Current, but from the Norwegian Trench.

Corten has used CPR data in a number of papers to test hypotheses concerning changes in Atlantic inflow and in the migrations, spawning locations and changing abundance of pelagic fish in the North Sea (e.g. Corten, 1999, 2000).

Taylor and Stephens (1980) first showed a correlation between zooplankton abundance and the position of the North Wall of the Gulf Stream off the east coast of North America. The occurrences of lower abundances of copepods in the Eastern Atlantic have coincided with southward shifts of the North Wall position and vice versa. They noted that the observed correlation implies an indirect link between the plankton and the Gulf Stream, as the two variables respond separately to changes in global atmospheric circulation. The relationship was shown to be robust, at least for the North Sea (Taylor, 1995; Hays, Carr, & Taylor, 1993), when the datasets were updated (Fig. 18) and it was suggested that the plankton are integrating a climatic signal that reflects displacements in storm tracks. Subsequent work has shown that the integrated response of the zooplankton is likely to be a consequence of changes in the timing of the spring phytoplankton bloom (Planque & Taylor, 1998). In the most recent development of this work, Taylor, Allen and Clark (2002) applied the ERSEM model (see below) and used the GSI as a probe to elucidate

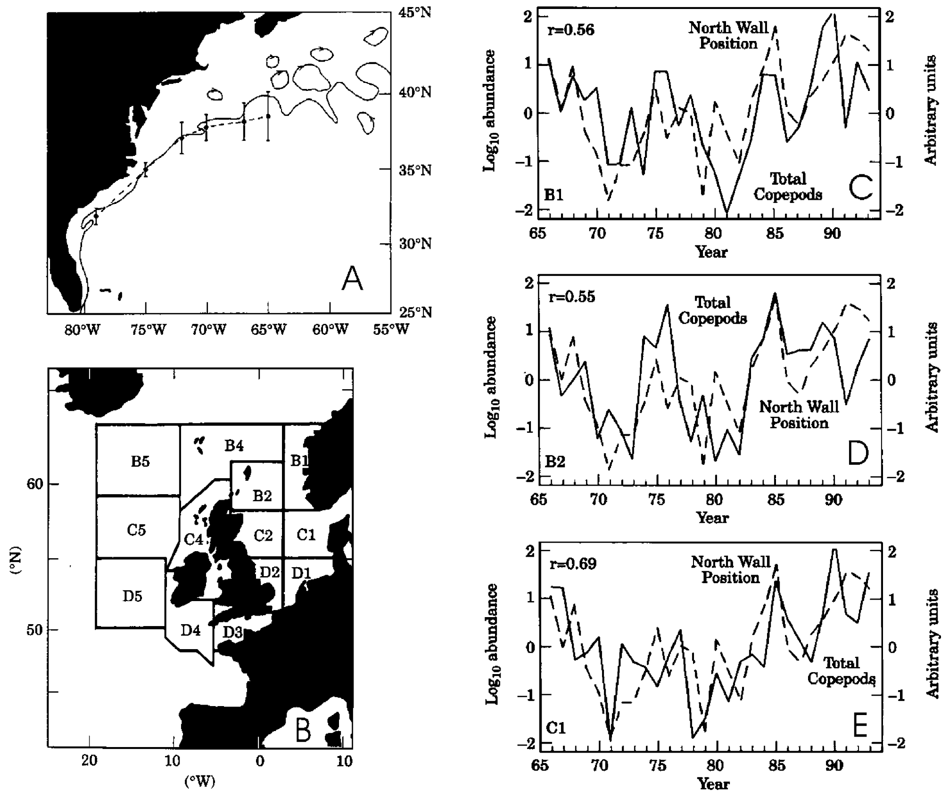


Fig. 18. (A) The position of the North Wall of the Gulf Stream and associated eddies in August 1984 with superimposed as a dashed line the mean position for the period 1966–1992. The error bars show two standard deviations to either side of the mean position. (B) Chart showing the positions of CPR Standard Areas. (C, D, E) Standardised graphs of the annual means of the latitude of the North Wall of the Gulf Stream (1966–1993 dashed line) with the logarithm of total copepods for three Standard Areas (B1, B2, C1). The correlation coefficient (r) between each pair of graphs is shown. Redrawn from Taylor (1995).

how biological systems can integrate subtle changes in a number of climatic variables that individually may not be the main driving forces for change in the plankton.

A new phase in the history of the survey was initiated by the discovery of a strong statistical relationship (Fig. 19) between the changing abundance of *C. finmarchicus* and *C. helgolandicus* in the waters around the British Isles, on the one hand, and an index of the North Atlantic Oscillation (NAO) on the other (Fromentin & Planque, 1996; Planque & Fromentin, 1996). These studies were fundamental to much subsequent research as they demonstrated a clear linkage between the dominant mode of atmospheric variability in the North Atlantic, the NAO, and plankton variability. The analyses involved novel approaches to the processing of data based on equal-area pixels, interpolation using kriging and new statistical techniques. However, the hypothesis that the reduction in *C. finmarchicus* in recent years was partially attributable to a decline and delay of the spring phytoplankton bloom cannot stand, as exactly the reverse has since occurred (see next paragraph). Further work has shown there to be regionally specific variability in seasonal and long-term changes in *C. finmarchicus*, that this species represents >50% of the zooplankton biomass over most of the North Atlantic and that it underwent a dramatic decline in biomass of 82% in the Northeast Atlantic between 1958 and 1997 (Planque & Batten, 2000; Planque, Hays, Ibañez, & Gamble, 1997). The relationship with the NAO was shown to break down in 1996 by Planque and Reid (1998). It was suggested by Reid, Edwards, Hunt, & Warner (1998a) and Reid, Planque, & Edwards (1998b) that observed linear trends in phytoplankton colour (Fig. 20) might reflect a response by the plankton to changing climate on a decadal scale. Edwards, Reid and Planque (2001) have examined the regional variability of phytoplankton biomass over the Northeast Atlantic in more detail and have shown that the different spatial responses are similar to the decadal patterns of change seen in sea-surface temperature. Exceptional oceanographic events, such as high or low oceanic inflow into the North Sea, were also shown to have an important effect on algal biomass. Data from the CPR have also been used to identify a regime shift (Fig. 21) in North Sea ecosystems circa 1988 (Reid, de Borges, & Svendsen, 2001a; Reid & Edwards, 2001) that appears to be linked to high transport of water in the slope current (Reid, Holliday, & Smyth, 2001).

A summary of CPR data for the periods 1959–1976 and 1991–1992, averaged for fishery assessment areas in the Northwest Atlantic, was produced by Myers, Barrowman, Mertz, Gamble and Hunt (1994). An analysis of results from the Scotian Shelf up to 1996 and comparison with physical data by Sameoto (2001) showed that statistically significant geographical and temporal changes had occurred in both zooplankton and phytoplankton between the two sampling periods. Conversi, Piontkovski and Hameed (2001) have demonstrated that abundance of *C. finmarchicus* in the Gulf of Maine was positively correlated with

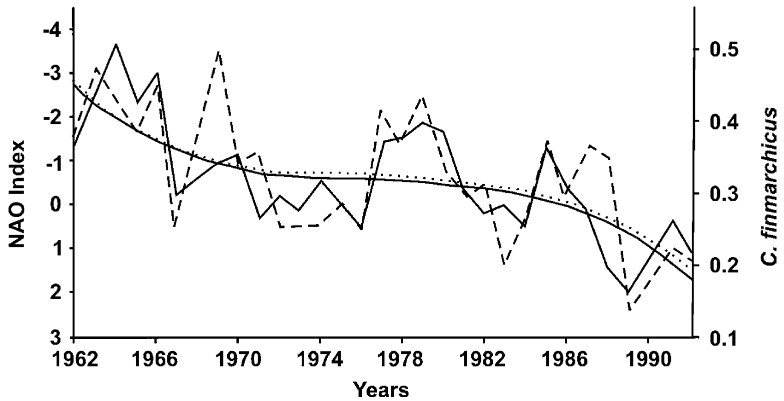


Fig. 19. Graphs of the average log abundance [log(x + 1)] of *Calanus finmarchicus* in the Northeast Atlantic (solid line) and the North Atlantic Oscillation index on a reverse scale (dashed line) from 1962–1992, with superimposed a third order polynomial fit. Redrawn from Fromentin and Planque (1996).

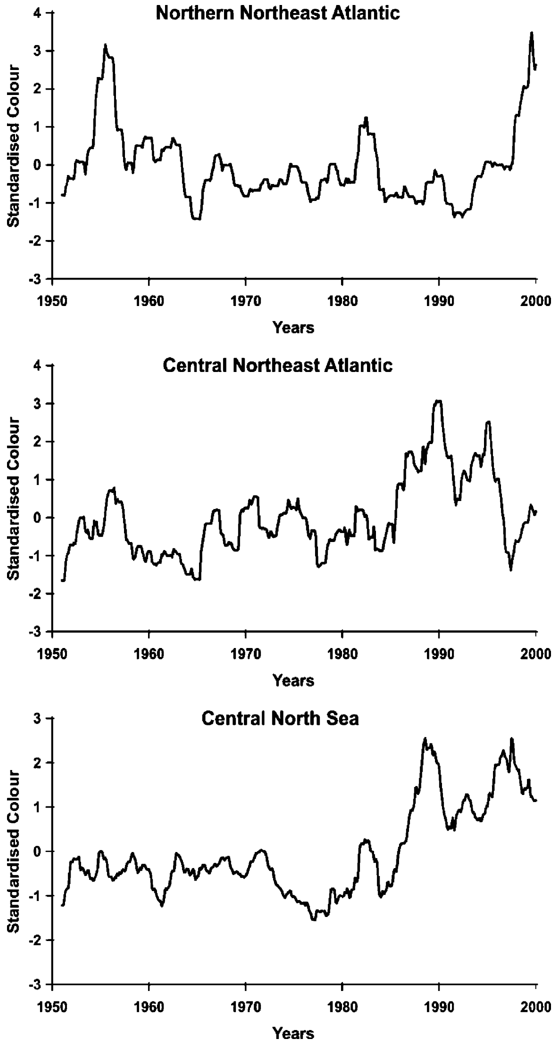


Fig. 20. Twelve-month moving average of standardised phytoplankton colour for the northern Northeast Atlantic, central Northeast Atlantic and the central North Sea (1950–2000). Redrawn and updated from Reid, Planque & Edwards, 1998b). See also Fig. 1 in Beare et al. (this volume) for an isopleth diagram of the same data.

the NAO index—the opposite relationship to that found on the other side of the North Atlantic by Fromentin and Planque (1996). Time series analysis was applied to the same data, which has a long 35-month sampling gap, by Licandro, Conversi, Ibañez and Jossi (2001). They were able to distinguish interannual and seasonal variability in the different taxa and found *C. finmarchicus* to be highly negatively correlated with low temperature. Earlier, Jossi and Goulet (1993) had reported that *C. finmarchicus* showed an increasing trend between 1961 and 1989 in sea areas off the east coast of the USA; other species showed no consistent pattern (see also Jossi, John & Sameoto (this volume)).

Johns, Edwards and Batten (2001) have described a southerly extension of Arctic calanoid copepods and the dinoflagellate *Ceratium arcticum* and an increase in their abundance in the Northwest Atlantic in the 1990s, which they attribute to the predominantly positive phase of the NAO during this period.

Results from the CPR survey have been used in a number of environmental assessment studies. For

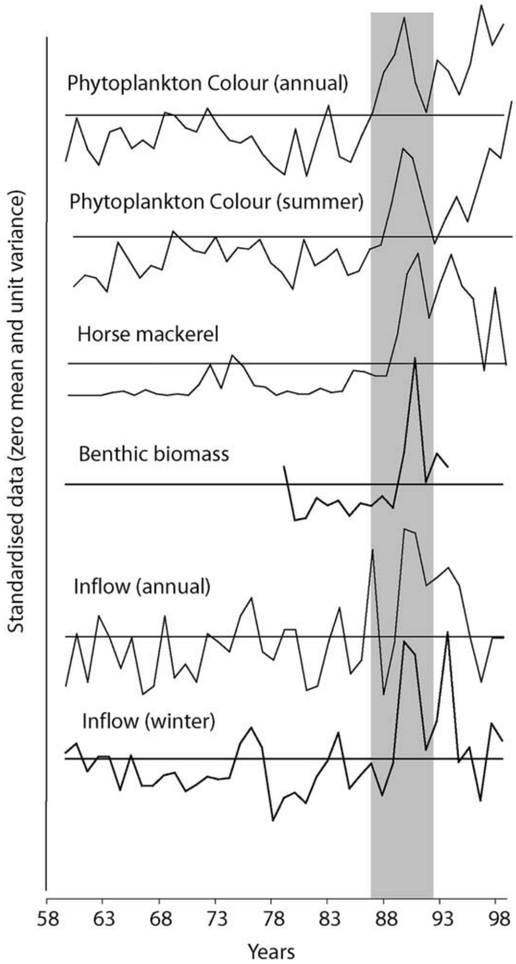


Fig. 21. Standardised graphs of phytoplankton colour (annual and summer, June–August means), annual horse mackerel landings in the North Sea (tonnes), benthic biomass off Nordeney in the Frisian Islands (Kröncke, personal communication) and modelled inflow (Sverdrup) of oceanic water into the North Sea (Morten Skogen, personal communication). Shaded area indicates the period of the regime shift, see Reid and Edwards (2001).

example Batten, Allen and Wotton (1998) investigated the effects of the *Sea Empress* oil spill on plankton communities in the Bristol and St George's Channels, and the survey results formed part of the North Sea Quality Status Report 1993 (NSTF, 1993) and contributed to the OSPAR (Convention for the Protection of the Marine Environment of the North-east Atlantic) Quality Status Reports 2000 (e.g. OSPAR Commission, 2000). Survey results have also contributed to process studies such as those by Boyd and Newton (1995), who showed that the sedimentation flux in part of the eastern Atlantic was much greater in 1989 than in 1990. Using data from the CPR they were able to demonstrate that larger diatoms settled faster than flagellates, leading to a more rapid 'biological pump'.

The survey has contributed to five projects of the European Commission's Marine Science and Technology (MAST) Programme (ERSEM, OMEX, MATER, NOWESP SEFOS), as well as contributing extensive and important data to ICOS and TASC (see above).

1. The European Regional Seas Ecosystem Model (ERSEM) project developed an ecosystem simulation

model of the North Sea. Data from the survey were used to derive counts of omnivorous and carnivorous mesozooplankton for each of the geographical boxes distinguished in the model (Broeckhuizen et al., 1995). In the second phase of the project, the seasonal dynamics of *C. finmarchicus* in the northern North Sea were modelled on the basis of CPR counts (Bryant, Heath, Gurney, Beare, & Robertson, 1997). The counts were used to derive prey concentrations for a model of the growth of four stocks of herring in the North Sea (Heath, Scott, & Bryant, 1997).
2. The Ocean Margin Exchange (OMEX) study focused on the processes controlling fluxes of water and matter across the European shelf, with a geographical emphasis in the first phase over the Goban Spur in the Celtic Sea and in the second phase off Iberia. The CPR data were used to place process studies at these sites in a temporal framework, to identify material contributing to pigments in traps and sediment samples, in grazing studies of mesozooplankton, and to determine the vertical variation of zooplankton biomass (Batten, Hirst, Hunter & Lampitt, 1999; Duinveld, Lavaleye, Berghuis, de Wilde, van der Weele, Kok et al., 1997; Joint, Wollast, Chou, Batten, Elskens, Edwards et al., 2001).
3. Between February 1997 and May 1999 a successful synoptic monthly CPR survey of the western Mediterranean took place for the first time between Genoa and the Strait of Gibraltar as part of the Mass Transfer and Ecosystem Response (MATER) project.
4. Results from the CPR formed an important contribution to the comprehensive compilation of data achieved during the North-west European Shelf Programme (NOWESP) research database project (Radach, Gekeler, Bot, Castaing, Colijn, Damm et al., 1996). This project focused on the quantification of biogeochemical fluxes; monthly mean data for temperature, salinity, nutrients, suspended matter, phytoplankton and zooplankton from eight locations were compiled and investigated (e.g. Bot, van Raaphorst, Batten, Laane, Philippart, Radach et al., 1996).
5. Participation in the Shelf Edge Fisheries and Oceanography Studies (SEFOS) project demonstrated a linkage between changes in fish stocks, inflow of oceanic water and CPR plankton (Reid, de Borges & Svendsen, 2001a).

Williams, Lindley, Hunt and Collins (1993) used multivariate analysis to distinguish communities of phytoplankton and zooplankton in the North Sea that were characteristic of mixed tidal waters and seasonally stratified waters. The communities demonstrated a strong coupling between the pelagic system and the benthos. Lindley, Gamble and Hunt (1995) reinforced this conclusion when they described an increasing trend in echinoderm larvae as a proportion of zooplankton over the Dogger Bank. They attributed the change to the effects of trawling on the benthos. The species richness of decapods with pelagic larvae showed a latitudinal gradient that decreased from south to north and temperature played a key role in their distribution and abundance (Lindley, 1998). Lindley and Batten (2002) built on these earlier studies on plankton diversity in a comparative study of four areas in the North Sea. They demonstrated there have been considerable changes through time, with an increase in the abundance of *Acartia* spp., meroplanktonic larvae and expatriate temporary residents of the holoplankton from warmer waters, with a consequent reduction in many holoplanktonic species. Their work drew attention to a difficulty in analysing biodiversity using CPR data. Because the adult benthic stages of meroplanktonic organisms can occupy a wide range of ecological niches, their species richness is likely to be much greater than that of the holoplankton; however, they are not easy to identify and are lumped together in routine CPR analysis, so their biodiversity is likely to be under-estimated.

An important new contribution to the interpretation of CPR data is a series of papers by Beaugrand and colleagues who have used new mapping, interpolation and statistical tools to resolve patterns of change in the plankton. For example, Beaugrand, Ibañez and Reid (2000) used three-mode PCA analysis which for the first time makes it possible to analyse variability of a range of physical variables in space and time concurrently with planktonic data. They confirmed that the planktonic communities of the English Channel and the Celtic Sea have been responding to the NAO in an opposite way to the communities in the Bay of Biscay. Beaugrand and Ibañez (2002) found that copepod diversity was negatively correlated with spatial dependence. This means that at small regional scales, where spatial variability changes rapidly, diversity is high and vice versa over large regions, such as the subarctic gyre where spatial change is less pronounced. The NAO was found to modulate both spatial dependence and diversity, showing a positive relationship in the northern North Sea and a negative one in the Atlantic to the west of the British Isles. A key methodological paper (Beaugrand & Edwards, 2001) used simulation and other mathematical techniques, such as diversity accumulation curves, to establish ways of applying biodiversity indices to CPR data. Using these techniques, Beaugrand, Reid, Ibañez and Planque (2000) mapped the biodiversity of calanoid copepods in the North Atlantic for the first time and demonstrated pronounced local variability. They observed a strong east–west asymmetry in biodiversity, which they attributed to the position, strength and path of the North Atlantic Current. Beaugrand, Ibañez and Lindley (2001) investigated the spatial change in diversity of calanoid copepods at diel and seasonal scales. The results were used to partition the North Atlantic into a number of regions with characteristic patterns of diversity that reflected current movements and hydrography (Fig. 22). Beaugrand, Ibañez, Lindley, & Reid (2002a) extended this work by identifying nine associations of species of calanoid copepods in the North Atlantic. Again, the patterns of distribution of the associations were seen to reflect the hydrography closely (Fig. 23). The most recent research (Beaugrand, Reid, Ibañez, Lindley, & Edwards (2002b) has shown a 10° latitudinal northward shift of warm-water copepods, with a corresponding retreat of cold-water species (Fig. 24). These changes were shown to be related to both an increasing trend in temperatures in the northern hemisphere (NHT) and to

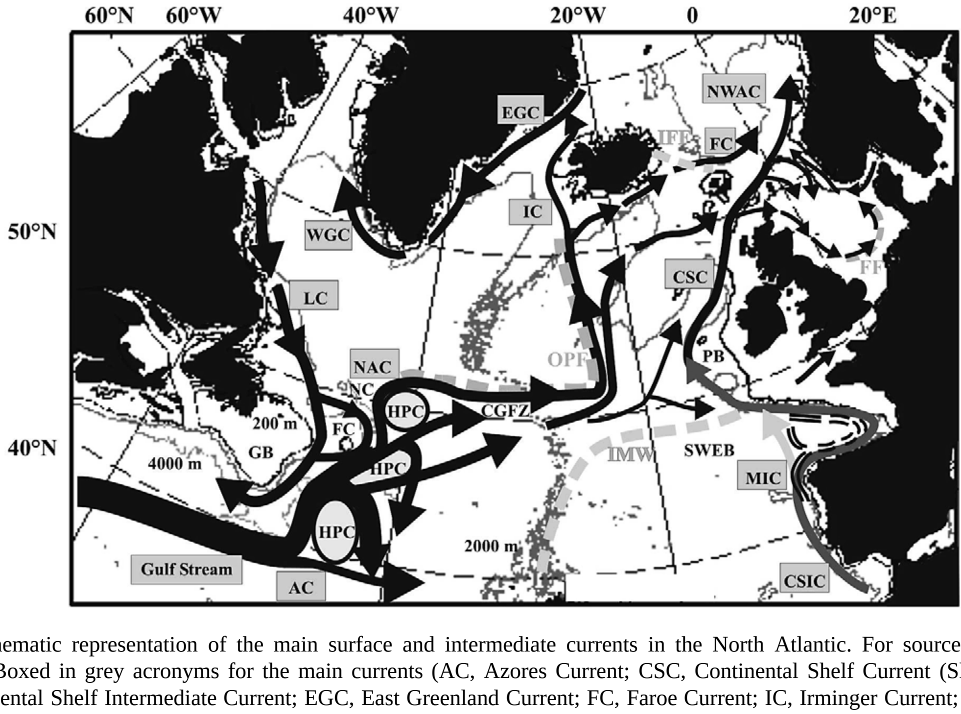


Fig. 22. Schematic representation of the main surface and intermediate currents in the North Atlantic. For sources see original publication. Boxed in grey acronyms for the main currents (AC, Azores Current; CSC, Continental Shelf Current (Slope Current); CSIC, Continental Shelf Intermediate Current; EGC, East Greenland Current; FC, Faroe Current; IC, Irminger Current; LC, Labrador Current; MIC, Mediterranean Intermediate Current; NAC, North Atlantic Current; NWAC, Norwegian Atlantic Current; WGC, Western Greenland Current. Lettering in light grey designating frontal structures (FF, Flamborough Front; IFF, Iceland–Faroe Front; OPF, Oceanic Polar Front. Other abbreviations (CGFZ, Charlie Gibbs Fracture Zone; FC, Flemish Cap; GB, Grand Banks; HPC, High Pressure Cells; IMW, Northern boundary of the influence of Mediterranean water (1100 m depth); NC, Northwest Corner; PB, Porcupine Bank; SWEB, Southwest European Basin. Modified from Beaugrand et al. (2001).

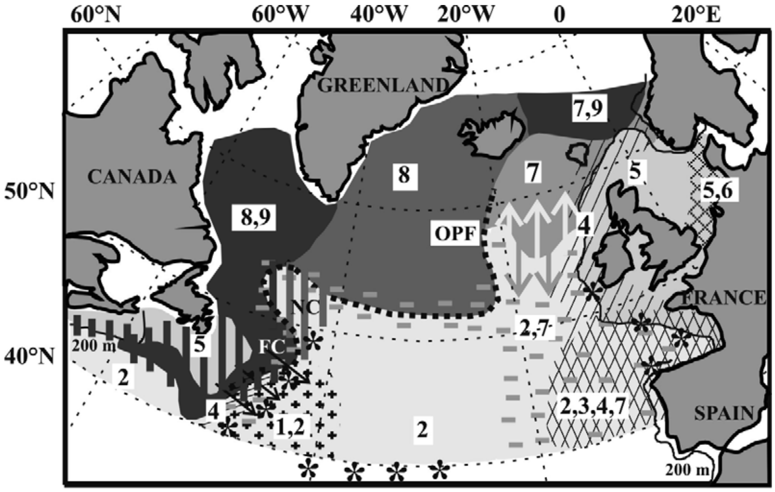


Fig. 23. A schematic map showing the centres of distribution of nine planktonic copepod species associations (bold numbers): 1, Subtropical and warm temperate association; 2, Warm temperate association; 3, Bay of Biscay and southern European shelf edge association; 4, European shelf edge association; 5, Shelf sea association; 6, Coastal association; 7, Temperate association; 8, Subarctic association; 9, Arctic association. In some areas, such as the Bay of Biscay some associations overlap. The asterisks show where rare species were found during the 40 years studied (1958–1997). Arrows indicate the seasonal progression of assemblages. A black dotted line indicates the position of the Oceanic Polar Front (OPF). Other abbreviations: FC, Flemish Cap; NC, Worthington's Northern Corner. Refer to the original publication for an explanation of the different patterns of shading. Figure modified from Beaugrand, Ibañez, Lindley & Reid, 2002a.

the NAO. The system in the eastern Atlantic affected in this way showed a high correlation between sea surface temperatures and NHT.

An important strength of the CPR survey has been its research on biogeography. A key part of this work has been a sequence of atlases the most recent of which (Edinburgh Oceanographic Laboratory, 1973) has been a standard reference source for 30 years. A new atlas has been produced using programmes developed by Gregory Beaugrand that take into account diel and seasonal variability in the plankton. It is intended that a hard copy and electronic version of this atlas will be published in the near future. A second atlas of North Sea plankton has been produced as a gridded interpolated dataset for ~110 species of phytoplankton and zooplankton on a CD using MATLAB software by Luigi Vezzulli (Vezzulli and Reid, this volume). Using the MATLAB template a microsoft-compatible version of the Vezzulli North Sea Atlas has been developed by the University of Plymouth Computing Department, with planned distribution as a CD and on the web in 2003.

A significant new development in the survey occurred in 2001 when Richard Kirby successfully extracted and amplified a mitochondrial DNA sequence for the first time from samples preserved in formalin in the CPR archive (Kirby & Reid, 2001). This breakthrough opens up the possibility of a completely new area of research based on the archive collection, which includes both analysed and non-analysed samples dating back to 1946. In particular, studies can be initiated on changes in the genetics of marine communities, especially larval meroplankton, which are difficult to identify. Fish larvae preserved in the CPR archive cover a period when huge changes have taken place in the composition and size of fish stocks as a result of heavy exploitation. Molecular information from these samples may provide evidence of the evolutionary response of populations through time to the fishery.

Much of the research reviewed in the previous sections has not been based on the principle of hypothesis testing. Instead, as observational science, the accumulating data have often told their own story and the unexpected has played a key role in resolving and understanding the complexities of plankton variability

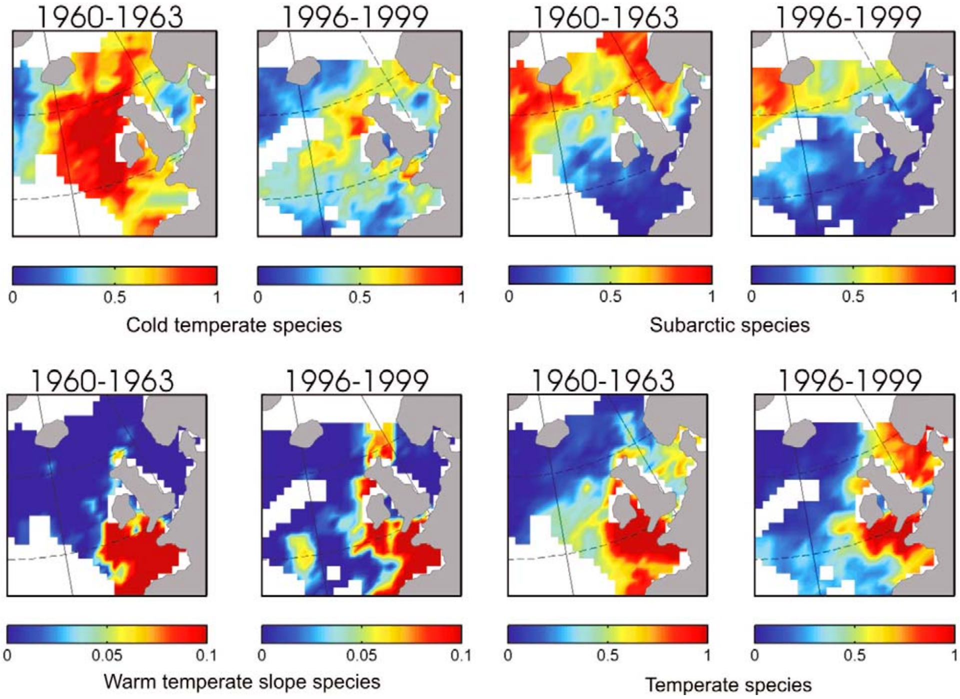


Fig. 24. Long-term changes in the mean number of species per copepod association as defined by Beaugrand, Reid, Ibañez, Lindley & Edwards, 2002b). Results are shown averaged over 4 years for the beginning (1960–1963) and the end (1996–1999) of the period studied and for four assemblages (cold temperate species, subarctic species, warm temperate slope species, and temperate species).

through time. The successful application of molecular technology is the latest example of the ever-increasing value of the CPR survey (see Dickson, 1995; Brander et al., this volume).

6. New technology

6.1. CPR performance trials

In the mid-1970s problems that had been experienced with the towing stability of CPRs because of the higher ship speeds were addressed in two projects at the Oceanographic Laboratory in Edinburgh: (1) to study towing and sampling performance; and (2) to design a new 'Fast CPR' (FCPR). The recently developed electronic temperature recorder, using miniature analogue tape recorders (MATRs) and fitted with depth, pitch, roll and flow sensors, was used to measure towing characteristics. Besides measurements on survey vessels, a programme of speed trials from 8 to 20 knots was carried out on the high-speed MV *Fathomer*, working out of Falmouth. Modifications to a standard CPR included changes to the diving plane, tail, fins, tail plane, 'fairings' to the nose and the side protuberances, extra nose ballast and variable height of towing point. Additional measurements of cable tension, cable angles, vibration and acceleration for the range of cable lengths and cable composition (man-made fibre ropes), gave a full description of towing characteristics for the standard and modified CPRs that were being tested. The suite of measurements showed that the standard CPR started to lose depth (from its normal depth of ~10 m) at speeds above 14 knots, frequently veering to one side of the vessel and 'jumping' out of the water, causing a large 'snatch-load' on the tow cable on re-entry.

The general conclusions of the comprehensive series of modifications, trials and measurements were three-fold:

1. The most significant modification to provide towing stability was a reduction in the width of the diving plane or its complete removal. However, this reduced the towing depth from the standard depth of 10 m to about 5 m; although to some extent this could be remedied by increasing the length of the towing cable.
2. Increasing the area of the tail fin or using twin tail fins were the most effective modifications for improving towing stability. Increasing weight at the nose, raising the height of the towing point, using a towing bridle, increasing the width of the tail plane or fairing (streamlining) the shape of the CPR body outline, had no significant effect.
3. Reducing the width of the diving plane and increasing the area of the tail fins accord with the theoretical considerations of the motion of towed bodies. With a horizontal or angled (nose-up) tail plane fitted between the two tail fins to form a ‘box-tail’, the loss of depth could be recovered by tilting the CPR nose-down, but this had a consequential effect on the flow rate through the recorder, as discussed below. Another significant observation from the trials was that the flow of water through the CPR, when horizontal, was almost exactly the 3 m^3/h expected through a 1.3×1.3 cm square orifice $\times$ 10 nautical miles. If the CPR was nose-up or nose-down, the area of the orifice presented to the flow was reduced and the flow diminished in proportion; a 10° change in pitch was equivalent to approximately a 10% reduction in flow.

Following the establishment of SAHFOS in 1990 a number of other performance trials of CPRs and associated instrumentation have been carried out. Details of these trials are given by Batten et al. (this volume).

6.2. Attached instrumentation

Technological developments associated with the CPR started in 1964 with the deployment of attached mechanical temperature recorders by Mr. William Brown on North Sea routes (Glover, 1967). The original mechanical thermograph (Braincon type 146) used a mercury-in-glass thermometer backed by a luminous strip (later changed to beta-lights). The results were recorded on photographic film that was advanced at approximately 5-mile intervals by a ratchet mechanism geared from the CPR impellor. Electronic temperature recorders, using miniature analogue tape recorders in the marine environmental recorder (MER) were introduced in 1975 (Aiken, 1977). The number of instruments deployed increased to include routes in the Irish Sea and English Channel, with some measurements on longer routes in the North Atlantic (Aiken, 1980). These electronic data-acquisition systems were powered by batteries and automatically activated by seawater switches.

In 1976/7, when the instrumentation section moved from Edinburgh to Plymouth, it was absorbed into the new IMER laboratory as a general service independent of the CPR survey. Some work continued on instrumented CPRs (Aiken & Halliday, 1980; Halliday, 1984). A suite of sensors was also developed to measure temperature, conductivity, depth, chlorophyll, turbidity, radiant energy, pitch, roll, vibration, acceleration and water flow, as well as solid-state data loggers (Aiken, 1980; Aiken, 1981a,b; Aiken & Bellan, 1986a; Williams & Aiken, 1990).

Aiken (1981b) designed a chlorophyll fluorescence sensor housed in a cylindrical pressure case for use in the FCPR and the Undulating Oceanographic Recorder (UOR) Mark 2. The instruments were attached to CPRs and used to compare tows of CPRs and UOR Mark 2 in the North Sea between November 1987 and May 1991 (Williams & Aiken, 1990; Williams & Lindley, 1992). The prototypes used in this research were developed commercially by Chelsea Instruments plc into a compact instrumentation package to which they gave the trade name Aquapack. The Aiken fluorometer differs from that of Chelsea Instruments in its use of a single rather than multiple pulsed system.

Since 1993, SAHFOS has deployed a number of Aquapacks attached to CPRs (see SAHFOS annual reports). Problems were initially experienced as a result of poor battery performance in cold conditions and electronics that were insufficiently robust for use on ships of opportunity. The CPR tows provided valuable trials to improve the performance of the instrument. In 1999 SAHFOS commissioned what is now Chelsea Technology Group Ltd to build a smaller ‘Minipack’ fluorometer and CTD for deployment on CPRs, with funding from the Department for Environment, Food and Rural Affairs (DEFRA). The development phase took much longer than expected as the prototype was not delivered to SAHFOS until June 2001 and was not fully operational until the summer of 2002; since then it has proved to be a compact and reliable instrument on a number of CPR tows.

Temperature recorders (Vemco Ltd) attached to CPRs have been deployed extensively since 1996 providing results with an accuracy of ±0.15 °C. Because of their built-in clock, they have proved particularly valuable as a check against hand-written log forms produced by the crew of towing ships.

In 1994, an electro-magnetic flow-meter was designed and constructed by Valeport Ltd in collaboration with SAHFOS; this measures water flow through the CPR without impedance. A number of these instruments were deployed on several routes in subsequent years. Results averaged for the period 1995–1998 (John et al., 2002) have confirmed that the mean volume filtered is 3.11 m^3 (s.d. ±0.8), which is close to the estimated volume of 3 m^3 based on the aperture area ×10 nautical miles. Clogging of the filtering silk by plankton does occur, but the overall effect on water flow is relatively small.

Other sensors, developed and deployed on CPRs and UORs measure bioluminescence (Aiken & Kelly, 1984), photosynthetically active radiation (PAR) and multi-spectral light (Aiken & Bellan, 1986a, 1986b, 1990); pH, dissolved oxygen, transmission, scattering and attenuation (Aiken, 1985; Aiken & Bellan, 1990), plus the Fast Repetition Rate Fluorometer (FRRF) (Behrenfeld, Bale, Kolber, Aiken, & Falkowski, 1996; Aiken, Rees, Hooker, Holligan, Bale, Robins et al., 2000; Aiken, 2001).

6.3. Prototype undulator

Because CPRs sample at a depth of ~10 m and high concentrations of plankton can occur below this horizon and perform vertical migration, experiments were initiated in the early 1960s to develop an undulating recorder (Glover, 1967). Hardy (1939:50) recognised the need for such a recorder to reduce the sampling artefacts associated with single-depth towing and he would have valued any measurements of the physical environment. The prototype used a mechanically geared tail plane, fitted between a pair of fins, to adjust the pitch of the towed body and to vary its depth (Fig. 25). The system was powered by an impellor and operated through a gear box, cranks and connecting rods that caused the angle of the tail plane to change. This resulted in quite irregular depth profiles because of the hydrodynamic forces needed to raise and lower the undulator in the water and to overcome the drag of the towing cable. Nevertheless, the prototype, which carried a standard CPR plankton sampling mechanism and mechanical depth recording device, was a significant test of the concept.

6.4. Undulating Oceanographic Recorder (UOR) Mark 1

In the late 1960s, development of the prototype undulator was hindered by a lack of appropriate electronic recording devices and sensors to monitor both the towing performance of the vehicle and environmental factors. For example, sensors for physics (temperature and salinity), chemistry (dissolved oxygen and inorganic nutrients), and biology (chlorophyll fluorescence, PAR and optical properties), needed to interpret plankton distributions, were not available. The Oceanographic Laboratory, Edinburgh, placed a contract with Plessey Marine Systems Unit (PMSU) in 1970, for an eight-channel digital tape recorder with sufficient

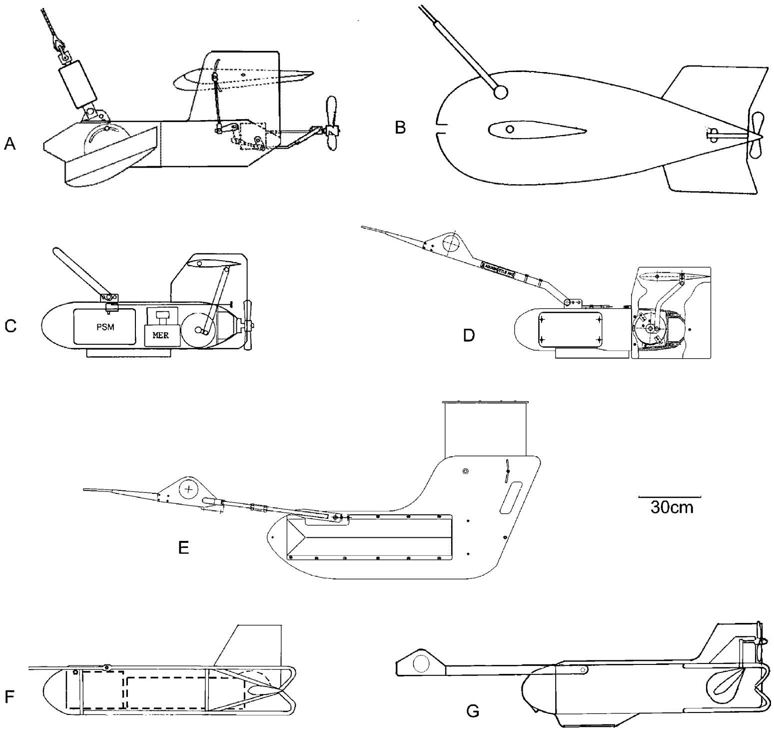


Fig. 25. Scale line drawings of the different types of Continuous Plankton and Environment Recorder in side view (A, Prototype undulator; B, Undulating Oceanographic Recorder Mark 1; C, Undulating Oceanographic Recorder Mark 2; D, Aquashuttle Mark III; E, Nu-tow; F, U-tow Mark 1; G, U-tow Mark 2).

data capacity for missions lasting several days or for 1000 miles. At the same time PMSU initiated a private venture to develop an undulating towed vehicle (UTV) with specifications suited to an undulating plankton recorder with a depth range of at least 5–75 m and no change of pitch with depth, a self-contained powered undulation mechanism and a self-contained electronic data logger with capacity for data from at least eight environmental sensors. After a few years of development and towing trials, the result was the Undulating Oceanographic Recorder (UOR) Mark 1 (Fig. 25).

The UOR Mark 1 was deployed from 1971 to 1976 in a variety of process cruises, with generally successful results and generating a wealth of operational experience (Bruce & Aiken, 1975; Aiken, Bruce & Lindley, 1977). Developments were carried out in collaboration with, and partly funded by, the US National Marine Fisheries Service Laboratory in Narragansett, Rhode Island, with some cruises on US vessels. Instrumented CPRs and UOR Mark 1 were deployed simultaneously in the international Fladen Ground Experiment 1976 (FLEX 76). FLEX 76 was designed to follow the spring bloom through to the spawning of the major zooplankton species (*Calanus* spp.) in early summer (data reported by Aiken & Williams, 1984). The large datasets generated during the experiment were used to drive the first generation of coupled hydrodynamic and biological production models.

6.5. Fast CPR (FCPR) and UOR Mark 2

The two main conclusions from the CPR high-speed trials (see above) became the guiding principles for designing the FCPR and subsequently the UOR Mark 2 (Fig. 25). The design of both machines did not include a diving plane to generate dive and lift forces; instead, in order to meet the need for extreme stability at high speed, large twin tail fins were attached to the body. An adjustable tail-plane fitted between the tail fins allowed the depth of the FCPR to be adjusted to a chosen fixed depth and was used to vary the depth of the UOR in undulating mode by means of a servo-mechanism. Both FCPR and UOR Mark 2 (Aiken, 1981a) were moulded to a monocoque design in glass-reinforced plastic (GRP). The body shell included a stainless steel sub-chassis and towing point with the same dimensions as the space used to house the plankton sampling mechanism (PSM) of a standard CPR. Thus a PSM from a CPR could easily be fitted and propelled by means of a standard CPR gearbox and impellor or later by a plastic corrosion-resistant gearbox and mini-impellor. Behind the area housing the PSM was 0.4 m^3 of space for electronic sensors and data loggers.

From 1977 to 1979, development switched from the fixed-depth FCPR to an undulating version, using the same body shell with a servo-controlled rear tail plane to achieve undulation. The aim was to achieve maximum performance, in terms of depth range and speed, given the size, weight and cable strength of the existing FCPR. As in the case of UOR Mark 1, the instrument was totally self-contained with an impellor-driven motorcycle alternator, which generated electrical power for the servo-control system at speeds of 8–20 knots. Throughout the trials and the early operations, most sensors and data devices were battery-powered for the sake of simplicity, though later studies in the North Sea used sensors powered directly from the alternator, with back-up from batteries. The development of UOR Mark 2 took less than 2 years and in early April 1979 the first successful tow from a commercial ship was completed on the MV *Cornouailles* (Brittany Ferries Limited) from Plymouth to Roscoff (Robinson, Aiken, & Hunt, 1986). As is the case with standard CPR deployments, the UOR Mark 2 was launched and recovered by the crew of the vessel at full speed (18 knots) using the CPR davit and standard 10 mm steel cable. The tow was completed satisfactorily, without any damage to the UOR, and data were acquired from a full suite of sensors (depth, temperature, chlorophyll fluorescence and light) over a depth range of 5–40 m and an undulation distance of about 1 nautical mile (2 km). In nearly all respects the tow was carried out as for a standard CPR deployment using a ship of opportunity, except that a scientist was present. This person attended to the deck instruments, recording cable tension, etc., throughout the tow, servicing the UOR instrumentation in France, changing logger and sensor batteries before repeating the procedure on the return voyage (Aiken, 1981a). Between 1977 and 1982, the UOR was deployed about 50 times on the PR route with about 75% success in data acquisition (Robinson, Aiken & Hunt, 1986). A feature of all these deployments was the first ever in situ measurements of chlorophyll fluorescence with simultaneous data on biological properties and physical structure obtained by a towed body using a ship of opportunity (Aiken, 1985).

After the first successful deployments of UOR Mark 2 in the Channel, the instrument was used to measure coupled physical and bio-optical properties on many research cruises in: the North and South Atlantic (including the Atlantic Meridional Transect between the UK and the Falkland Islands), north-west European shelf seas, the Iceland, Norwegian, Barents and Mediterranean Seas and the Indian, Antarctic and Pacific Oceans. The machine and its attached instruments proved particularly useful in providing sea-truth data to calibrate remotely sensed data from satellites (Aiken, 1985) and it has been proposed, in combination with CPRs, as a means of monitoring Large Marine Ecosystems (LMEs) (Williams & Lindley, 1998). A comparison between instrumented CPRs and UORs has been carried out by Lindley and Williams (1994) in the North Sea between 1988 and 1991. This showed that discontinuities in temperature, salinity and turbidity, which mark the positions of fronts, were reflected in the geographical patterns of plankton assemblages. Many other publications have been derived from the above cruises, some of which are listed in a separate bibliography on the SAHFOS web site.

6.6. Aquashuttle, Nu-tow and autonomous plankton sampler

In 1985, Chelsea Instruments plc negotiated an agreement with PML to develop a commercial version of UOR Mark 2 called the Aquashuttle. Three versions of this machine were subsequently developed increasing in size from 36 to 40 and eventually to 50 cm wide to enable them to carry an increased payload. Aquashuttle Mark III (Fig. 25) is capable of operating at speeds of 8–25 knots and down to depths >120 m with a faired cable.

As a further development of UOR technology a new machine called Nu-tow, with a prefabricated body, instead of a moulded glass-fibre one, (Fig. 25) was developed in 1996/7 by PML for Chelsea Instruments with funding from the UK Department of Trade and Industry (DTI). In this machine polyethylene panels are attached to a stainless steel frame that encloses a 100-litre cargo hold. The machine is capable of operating at speeds of 5–15 knots, can undulate down to depths of ~80 m with unfaired cable and can carry a wide range of instruments. Data from these can be stored in solid-state memory systems or passed up a cable to a shipboard computer, which can be used in real time to control the pattern and depth of undulation. The use of Nu-tow in regular monthly monitoring of Narragansett Bay has been described by Berman and Sherman (2001).

An autonomous plankton sampler (APS) was designed and built by Chelsea Instruments in partnership with PML as a substitute for the PSM used in the CPR. The APS closely matches the size and other characteristics of the CPR PSM and can use silk or nylon filtering gauze, but this is advanced at stepped intervals instead of continuously. The APS includes a data-logging system for six external sensors and a system for advancing the gauze from an external sensor.

6.7. U- tow and Aquamonitor

When SAHFOS was established there was a need to produce a low-cost alternative to the CPR that could undulate to ~50 m depth at ‘high speeds’ and carry a range of sensors, as well as a plankton sampling unit. In 1993 DEFRA provided the necessary funding for Valeport Ltd, in conjunction with SAHFOS and later the Department of Agriculture for Northern Ireland (DANI) and the Centre for Environment, Fisheries and Aquaculture (CEFAS), to develop U-tow Mark 1 (Fig. 25); a series of trials of the sampling and sensing system was carried out between 1994 and 1997 (Hays, Walne, & Quartley, 1998; Hays, Clark, Walne, & Warner, 2001; Mills, Walne, Reid, & Heaney, 1998).

In April 1997, W. S. Ocean Systems Ltd. purchased the U-tow design from Valeport Ltd. This caused a delay as the new company redesigned both the machine body and the supporting software systems. The first U-tow Mark 2 (Fig. 25) was delivered in May 1998 and underwent a long series of development trials (see SAHFOS annual reports). These trials ended successfully in September 2002, when a fully operational system was towed in undulating mode across the northern North Sea on the SC *Aberdeen* at 16 knots. On that occasion the machine housed a plankton sampler and a microplankton sampler (‘Aquamonitor’, see below), and it measured fluorescence, conductivity, temperature, PAR and depth. The resulting data were passed up a cable and displayed in real time on a computer. Two-way communication enables the operator to adjust the undulation characteristics of the vehicle and vary the sampling frequency. An alternative system for storing information on a marine data logger within the towed body is also available.

The microplankton sampler mentioned above was designed and built by W. S. Oceans Ltd as part of the development contract for U-tow and given the trade name, Aquamonitor. It is constructed around a programmable syringe with a conditional sampling protocol and can collect up to 52 water samples of 200 ml, which are stored individually in plastic medical reagent bags.

7. The future

The CPR survey is a testament to the imagination, foresight, design and technical skills of the late Sir Alister Hardy. In this paper we have traced the history of the survey and given an account of various vicissitudes in the course of its development. Its survival over such a long period of time is a result of the dedication of the staff, especially the analysis and workshop teams. One of the key reasons for the success of the CPR survey has been its continuity and the overlap of staff, with each generation passing on its expertise to the next. It is, however, the research output of the survey that has maintained the scientific profile that was needed for UK Government funding from 1931 until SAHFOS was established in 1990. Over that period the priorities of the funding agencies changed on several occasions so that at times the objectives of the survey were marginal to their interests. However, since 1990 the survey has become a not-for-profit charity supported by an international consortium. Throughout this period, funding from UK government agencies has continued to provide approximately 60% of the total support. In any 1 year, more than 20 separate contracts may be operational. The complexity of this funding mechanism, which is highly dependent on the immediate priorities of various governments, gives rise to an inherent financial insecurity and the survey has come close to closure at times over the last 20 years. There is a need to find new ways of ensuring the long-term funding of the CPR survey and other international monitoring programmes of global importance.

The oceans are an “essential component of the global life support system” (UNCED, 1992) and plankton is a critical part of this system: it is the basic food for almost all life in the sea and it plays a key role in climate change, for example through the carbon cycle. An important outcome from the UN Conference on Environment and Development (UNCED) in Rio de Janeiro in 1992 was Chapter 17 of Agenda 21, on the Protection of the Oceans, which may be considered a ‘Magna Carta’ for the protection, sustainable development, management and prediction of change in the oceans. The declaration distinguishes between the ‘high seas’ and ‘waters that are under national jurisdiction’. In the decade since it was published there has been a far-reaching reassessment by governments of their policies on marine issues and a new recognition of the importance of systematic observations, long-term datasets and open access to information. To quote from the UNCED Declaration (1992): “Information for management purposes should receive priority support in view of the intensity and magnitude of the changes occurring in the coastal and marine areas”. The Declaration also noted the need to identify “ongoing and planned programmes of systematic observation of the marine environment, with a view to integrating activities and establishing priorities to address critical uncertainties for oceans and all seas”. On the basis of the research findings presented in this overview, the CPR survey, possibly the longest running, large-scale marine biological survey in the world, is making a major contribution to tackling these uncertainties. Three other areas identified as priorities in the Declaration, namely developing tools to determine marine biodiversity, identifying indicators of environmental status and contributing to periodic assessments, are important aspects of the survey. Hardy was clearly far ahead of his time in establishing an operational plankton survey more than 70 years ago to map plankton distribution synoptically, to relate these patterns to living marine resources and to use them to develop an understanding of climate change.

It has been shown that the value of long-term time series increases progressively with the addition of data from each new year (Dickson, 1995; Brander et al., this volume). This has been well demonstrated by the CPR survey as the range of new applications for the data has been identified as the time series has lengthened. Data and descriptions are the essential foundation for the construction and testing of hypotheses. In the case of the CPR however, especially with the advent of computer analysis, the data have been used in a number of cases to tell their own story, often revealing unexpected findings. The original concepts for the survey as outlined by Hardy in 1939, namely synoptic monthly mapping, finding the best locations at which to fish, strengthening the economics of the fishery, a better understanding of the biology of the North Sea, relating plankton to hydrography, assessment of climate change, phenological studies and the production of operational products, have all come to fruition in varying degrees. The growing value of the dataset is seen in the many new applications that have recently been achieved or can now be envisaged in the future. Recent or ongoing applications include input to models and their validation, providing sea-truth data for satellite observations, use of the data in the development of statistical and presentational methods, development of indicators of ecosystem change, providing the spatial and temporal background for large process studies, in the design and operation of monitoring programmes, in the use of molecular techniques, in environmental management and as a valuable contribution to quality status reports.

Sustainable management is a key objective in the UNCED Declaration. One approach to the management of oceanic ecosystems was proposed by Reid in 1999. He suggested, first, that the oceans should be classified into regions with similar hydrographic and biological characteristics; secondly, that a monitoring strategy should be implemented in these regions; and, thirdly, that periodic regional assessments should be carried out in the same areas. Two principal approaches to classifying oceanic ecosystems exist at present, one based on hydrography and phytoplankton production (Longhurst, 1998) and the other on hydrography, productivity and ecological carrying capacity (Shermann, 1994). The classification of four biomes and 56 provinces, as proposed by Longhurst is analogous to the biomes based on representative vegetational types, as used in the classification of terrestrial ecosystems. Shermann (1994) divided the coastal margins of the continents into 50 large marine ecosystems (LMEs). More recently, Shermann and Duda (1999) have proposed a modular ecosystem approach to the management of LMEs. This approach includes a productivity module in which the monitoring of zooplankton by means of CPRs or CPERs is an important component of the management system. This recognition of the key role that zooplankton plays in coastal and oceanic ecosystems as grazers and as the main food for fish larvae, young fish and many pelagic fish is being addressed by Global Ocean Ecosystem Dynamics (GLOBEC). SAHFOS is affiliated to this international programme, which aims to determine how global change will affect the abundance, diversity and productivity of marine populations.

The Earth is a blue planet of oceans with water covering 361,000,000 km^2; monitoring this huge area for management purposes means that a completely new strategy needs to be developed. Reflecting the distinction made by UNCED between ‘coastal seas’ and the ‘high seas’, the Global Ocean Observing System (GOOS), which has been strongly endorsed by UNCED, has developed parallel monitoring strategies, one led by the ‘Ocean Observations Panel for Climate’ (OOPC) and the other by the ‘Coastal Oceans Observations Panel’ (COOP). The CPR survey is part of the Initial Observing System of GOOS and its results are relevant to both panels. The major emphasis on biological processes, however, will lie with the coastal module. A new monitoring strategy within GOOS, including a ‘Living Marine Resources’ component that will systematically monitor the plankton of the oceans, has been under discussion for some time. As might be expected, the plans for COOP are focused on physical and chemical aspects of monitoring, but there is an urgent need to establish a global programme of plankton monitoring in order to address the concerns of UNCED over the changes that are evident in the oceans and the impact they may have on biodiversity and living marine resources.

At present most plankton-monitoring programmes are based at single locations and do not obtain samples throughout the year. Few have extended for more than 3 years and there is no monitoring at all over very large areas of the ocean. As Duarte, Cebrian and Marba (1992) have shown that although many long-term monitoring programmes have been started, few survive more than a few years. Colijn (1998), in his introductory text to the special publication covering the ICES symposium on ‘The temporal variability of plankton and their physico-chemical environment’, also said that many time-series studies are in danger of closure either for financial reasons or because key trained staff are not being replaced. To quote from Colijn “This paradoxical situation is emerging exactly at a time when time series observations are urgently needed to resolve global change issues and to help distinguish effects due to anthropogenic variation from those attributable to natural variation”. Only two surveys (CPR and the California Cooperative Oceanic Fisheries Investigations, CalCOFI) exist that monitor extensive areas of the coastal and high seas on at least a monthly basis (for the latter see Rebstock, 2001). Of the two programmes, only the CPR survey operates at an ocean-basin scale. Other long-term programmes, such as the Southern Ocean CPR survey (Hosie et al., this volume) and along the west coast of South Africa (Verheye & Richardson, 1998), do not operate all year round. Long-term studies of the vertical variability of plankton in the oceans are only being carried out systematically at two stations, namely Station ALOHA in the Pacific (Hawaii Ocean

Time Series, HOTS) and in the Atlantic (Bermuda Atlantic Time series Study, BATS) (Landry, Al-Mutairi, Selph, Christensen, & Nunnery, 2001; Madin, Horgan, & Steinberg, 2001).

There is therefore a need to develop a network of transects that will sample the key provinces or LMEs identified by Longhurst and Sherman. The information obtained will be essential for the regional assessments that will be needed, in response to UNCED, for the Regional Seas Programme of the United Nations Environment Programme (UNEP) and associated regional conventions, such as the Convention for the Conservation of Antarctic Marine Living Marine Resources (CCAMLR), the Convention for the Protection of the Marine Environment of the North-east Atlantic (OSPAR), the Convention on the Protection of the Marine Environment of the Baltic Sea area (HELCOM), and the Convention for the Protection of the Mediterranean Sea against Pollution (Barcelona).

The only cost-effective way to establish such regional plankton monitoring programmes is by using ships of opportunity. Extensive areas of the oceans are already covered by voluntary observing ships operating 'expendable bathythermographs' (XBTs) to monitor temperature, as part of the programme of the World Meteorological Organisation (WMO), and some routes are also being used to monitor CO_2 (Anon, 2000). Plankton sampling should make use of the same ships wherever possible. In the development of plans for monitoring large marine ecosystems and extensive oceanic areas in GOOS the CPR approach is recognised as a practical means of rapidly surveying large areas for plankton; the approach has already been recommended by GOOS for adoption in new regional surveys. Such use of CPRs would make regional comparisons possible, standard methodology is already in place to guarantee quality, and a wealth of advice is available. In some regions new surveys may use Continuous Plankton and Environmental Recorders (CPERs) that can measure many physical and chemical characteristics of the water at the same time (see Section 6, New technology). Since the cost of setting up such programmes and carrying out the analysis is a severe constraint at present, development of cheaper technologies, manufacture of low-cost sampling systems and rapid analysis of samples are needed in order to bring costs down.

Establishing new regional CPR programmes will not be easy as is evident from past experience where a number of attempts have been made to establish surveys elsewhere in the world. In the case of an attempt to run a survey in the Gulf of Guinea, it was a lack of funding for local infrastructure that prevented its continuation despite a full programme of sampling having taken place over a number of years. This underlines the need for capacity building and full funding if surveys are to develop satisfactorily in underdeveloped parts of the world. In addition to the SAHFOS CPR survey, two other CPR surveys exist at present. The Narragansett survey inherited a programme that had been started from Edinburgh, and the Southern Ocean Survey (Hosie et al., this volume) makes use of research and supply ships on their way to and from Australian and Japanese Antarctic bases. The main reasons for failure to set up other surveys have been a lack of recognition of the essential need of technical and logistical back-up, difficulty in adapting to the specialised nature of the plankton analysis, and problems over training and staffing. These points must be taken into account whenever new surveys are established and standard methodology must be adopted. A Working Group (No. 115) has been established by the Scientific Committee on Oceanic Research (SCOR) on 'Standards for the survey and analysis of plankton' in order to address these issues. The working group has been given a four-fold remit:

1. To review present methods of collection, analysis and curation of plankton samples;
2. To evaluate sampling strategies and different instrumental approaches to the measurement of plankton;
3. To propose a methodology for comparison and intercalibration of different sampling systems;
4. To recommend a standard package of measurements that should be taken in conjunction with plankton surveys to enhance the resulting products.

As new surveys are established improved quality control may be achieved through exchange of personnel and by 'ring-testing' of samples. Careful consideration must also be given to determining the appropriate number of samples to be analysed and where sampling should best be carried out when surveys are being designed (see Planque & Reid, 1998).

The main remit of SAHFOS as it moves further into the 21st century is to maintain a comparable and consistent survey in the North Atlantic, and where and when possible expand into adjacent areas, such as the Norwegian, Labrador and Barents Seas, which are all important areas in studies of climate change. A second aim is to promote and sustain the new Northeast Pacific survey. The two surveys are expected to work closely together in the future, gaining strength from the standardisation of measurements and data recording, which are making it possible to draw comparisons between the Atlantic and the Pacific Oceans. Thirdly, SAHFOS proposes to develop new instrumentation for attachment to CPRs in order to measure other variables in addition to plankton and to apply molecular techniques in sample analysis. Fourthly, SAHFOS will continue to appraise ways to improve access to and rapid dissemination of data through on-line access to the database. Finally, SAHFOS will promote the establishment of other regional surveys with the aim of achieving global coverage. There will be many hurdles to overcome before all these objectives are achieved, and a flexible approach will be needed in response to changing priorities in national and international science policy.

We are confident that the value of the CPR time series will continue to increase into the future. Key issues for the next decade are likely to include: climate change, fisheries applications as input to new stock-assessment models, biodiversity, eutrophication, EU directives on habitats and water, the nutritional state of phytoplankton, molecular genetics, introduced species, mesoscale variability and applications to modelling the global climate. There is strong evidence that we are living through a time of dynamic change related to global warming, with rapid rises in global temperatures expected over the next 100 years. The oceans already appear to be responding to this warming trend (Levitus et al., 2001; Beaugrand, Reid, Ibañez, Lindley & Edwards, 2002b), and data from the CPR survey are likely to provide important benchmarks against which to assess the scale and speed of response of ecosystems to future change. If the last 70 years are anything to go by, the survey will continue to provide the basis for a wide range of exciting research. The legacy of Sir Alister Hardy is indeed great.

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We gratefully thank the captains and crews of the many ships that have deployed CPRs in a voluntary capacity and the support given by ship owners and management companies, charterers, port staff stevedores and agents without which this 70th anniversary review would not have been possible. Since the first tow in June 1931 more than 214 vessels have assisted in the operation of the survey. The ships and companies that towed CPRs in the anniversary year 2001 are listed in Table 2. Since the survey started in 1931 close to 100 plankton analysts (Table 3) have contributed to the processing of CPR samples. We are indebted to all past members of the analysis, workshop and administrative teams for the contributions they have made to the CPR time series. Especial thanks are due to Julie Finlayson, Johanna Sidey, Darren Stevens and Marion Smith for help with the bibliography, figures and proof reading. Staff of the National Marine Biological Library, and in particular Emma Woodason, provided considerable assistance in literature searches. Prior to 1991 the survey was funded by UK Government agencies; from the establishment of SAHFOS funding has derived from an international consortium that in 2001 included IOC, UK DEFRA, UK DTI, UK NERC, UK CEFAS, USA NSF (Woods Hole Laboratory), USA University of Alaska, Canada DFO, Faroese Fisheries Laboratory, IFREMER France, Marine Institute Ireland, a consortium of Netherlands Government institutes, Netherlands RIKZ, Ministry of Fisheries Denmark and The Atlantic Salmon Trust. We are indebted to all our funders, past and present, for their continuing strong support.

Table 2
Routes, towing vessels, shipping companies and charterers that towed CPRs in 2001

Route	Towing vessels	Shipping company
A	*St. Clair*	P&O Scottish Ferries Ltd
Pacific AC	*Polar Alaska*	Polar Tankers Inc
BA, BB, BC, BD	*Prince of Tides Santa Lucia*	Scaldis Reefer Chartering, Seatrade, S.A., Charterers, Geest Bananas Ltd
C	*Tor Selandia*	DFDS -Tor Line AB
C North	*Cometa*	Sea Cargo A/S
D, DA	*CAST Performance*	CAST Europe BV
EB, EA, LR, V, Z, ZB, ZC	*Skogafoss, Selfoss*	Eimskipafelag, Icelandic Steam Shipping Company
HE, LG	*Tor Cimbria, Tor Flandria*	DFDS-Tor Line
IB	*Pelayo* renamed *City of Oporto*	Owners: Kapitan Mänfred Draxl Schiffarts GmbH. Charterers, Andrew Weir Shipping Ltd
IN	*European Ambassador*	P&O European Ferries (Irish Sea) Ltd
M	*Cometa Tungenes,* renamed *SC Aberdeen*	Nor-Cargo Group A/S, Hagland Shipping A/S, Nor-Cargo then Sea Cargo A/S
R	*Maersk Flanders*	Norfolk Line Ltd., Norfolk Line BV
SA	*City of Manchester, Pacheco*	Andrew Weir Shipping Ltd
Pacific VJ	*Skaubryn*	Seaboard International Shipping Company
W	*CAST Performance*	CAST Europe BV

Table 3
List of CPR analysts over the period 1931–2002 ordered by the year when they first started to analyse with, where known, the year they finished analysing

Year started	Year finished	Name of analyst
1925		A.H. Hardy
1931	1935	J.H. Fraser
1932	1946	C.E. Lucas
1933	1947	G.T.D. Henderson
1933	1948	K.M. Rae
1938	1956	C.B. Rees
1938	1947	N.B. Marshall
1938	1939	W. Macnae
1946	1950	R.S. Glover
1946	1978	Miss D.E. John
1946	1947	A. Saville
1946	1947	Miss D.E. Williams
1947	1954	Miss M.F. Jobson
1947	1977	G.A. Cooper
1948	1958	F.R. Vane
1949	1951	H.R. Schurr
1949	1971	W.W. Brown
1951	1970	G.A. Robinson
1952	1953	D.A. Priest
1954	1956	D.H. Mills
1956	1971	J.M. Colebrook
1956	1960	Miss B.I. Barnes

(*continued on next page*)

Table 3 (*continued*)

Year started	Year finished	Name of analyst
1957	1959	B.M. Bary
1959	1964	V. Bainbridge
1960	1962	Miss D.R. Pearson
1960	1976	D.H. Jones
1960	1974	L.T. Jones
1960	1998	H.G. Hunt
1961	1967	J.B.L. Matthews
1962	1992	J. Roskell
1962	1963	S.R. Geiger
1962	1963	A.E. Robertson
1964	1966	W.J. Beasleigh
1964	1965	G.A. Yarranton
1964	1974	G.N.L.I. Melville-Mason
1965	1966	Miss D.J. Colebourne
1965	1967	R.H. McHardy
1965	1965	B. Zeitschel
1965	1969	Miss B.J. McKay
1966	1967	D.W. Canning
1966	1969	D.J. Lowson
1966	1967	S. Lakkis
1967	#	A.W.G. John
1967	1972	C.M. Lee
1967	1970	F.C. McNaughton
1967	1970	R. Williams
1969	1976	Miss R.J. Harper
1969	#	J.A. Lindley
1970	1972	J.A. Booth
1970	1971	S.T. Hull
1970	1971	Miss V. Legge
1970	1973	P.J.B. Hart
1970	1972	C.C.E. Hopkins
1972	1975	Mrs M.A. Wallace
1973	1977	S.H. Coombs
1973	1977	P.C. Reid
1974	1978	D.E. Smith (NMFS)
1975	1977	A.R. Hiby
1975	1981	Ms S. Surey-Gent
1975	1984	H.H. Bottrell
1976	1980	R.K. Pipe
1977	1978	D.B. Robins
1977	1978	Mrs M.D. Brinsley
1977	1990	N.C. Halliday
1977	1979	H.G. Langworthy
1977	1978	A.J. Mullen
1977	1983	J.A. Stephens
1977	1988	Mrs C.E. Mitchell
1977	#	Mrs T.D. Jonas
1980	1983	Miss C.M. Hoyle
1980	1983	Miss C.A. Fosh
1983	1988	N.R. Collins
1989	1999	A.J. Warner
1991	1996	Miss C.A. Proctor
1992	1994	G. Hays

(*continued on next page*)

Table 3 (*continued*)

Year started	Year finished	Name of analyst
1992	#	Miss C.O.M. Wotton
1994	#	Dr S.D. Batten
1994	#	A.W. Walne
1994	#	Miss J. Finlayson
1995	#	P.R.G. Tranter
1995	1998	Miss R.J.S. Allen
1995	#	M. Edwards
1997	#	D.G. Johns
1998	1999	L. Vezzulli
1999	#	C. Buckland
1999	#	J. Wright
2000	#	J. Sidey
2002	#	A. Richardson
2002	#	G. Beaugrand
2002	#	M. Wooton

Analysts working in 2002 marked by #.

References

Anon (2000). IOC-SCOR Ocean CO_2 advisory panel, First Session, Paris France 4–6 September 2000. Intergovernmental Oceanographic Commission. *Reports of Meetings of Experts and Equivalent Bodies, 171*, 1–29.

Aebischer, N. J., Coulson, J. C., & Colebrook, J. M. (1990). Parallel long-term trends across four marine trophic levels and weather. *Nature London*, *347*, 753–755.

Aiken, J. (1977). Temperature measurements with the CPR during 1975. *Annales Biologique Copenhagen*, *32*, 28–29.

Aiken, J. (1980). A marine environmental recorder. *Marine Biology, 57*, 238–240.

Aiken, J. (1981a). The Undulating Oceanographic Recorder Mark 2. *Journal of Plankton Research*, *3*, 551–560.

Aiken, J. (1981b). A chlorophyll sensor for automatic, remote operation in the marine environment. *Marine Ecology Progress Series*, *4*, 235–239.

Aiken, J. (1985). The Undulating Oceanographic Recorder Mark 2. A multirole oceanographic sampler for mapping and modelling the biophysical marine environment. In A. Zirino (Ed.), *Mapping strategies in chemical oceanography* (pp. 315–332). Washington, DC: American Chemical Society Advances in Chemistry Series, 209.

Aiken, J. (2001). Fluorometry as a biological sensor. In J. H. Steele, K. K. Turekian, & S. A. Thorpe (Eds.), *Encyclopaedia of Ocean Sciences* (pp. 1073–1081). San Diego, CA: Academic Press.

Aiken, J., & Bellan, I. (1986a). A simple hemispherical logarithmic light sensor. *Proceedings of the Society of Photo-Optical Instrumentation Engineers SPIE, 637, Ocean Optics*, *8*, 211–216.

Aiken, J., & Bellan, I. (1986b). Synoptic optical oceanography with the undulating oceanographic recorder. *Proceedings of the Society of Photo-Optical Instrumentation Engineers SPIE, 637, Ocean Optics*, *8*, 221–229.

Aiken, J., & Bellan, I. (1990). Optical oceanography: an assessment of a towed method. In P. J. Herring, A. K. Campbell, M. Whitfield, & L. Maddock (Eds.), *Light and life in the sea* (pp. 39–57). Cambridge: Cambridge University Press.

Aiken, J., Bruce, R. H., & Lindley, J. A. (1977). Ecological investigations with the undulating oceanographic recorder: the hydrography and plankton of the waters adjacent to the Orkney and Shetland Islands. *Marine Biology*, *39*, 77–91.

Aiken, J., & Halliday, N. C. (1980). Temperature measurements with the Continuous Plankton Recorder in 1978. *Annales Biologiques*, *35*, 70–71.

Aiken, J., & Kelly, J. (1984). A solid state sensor for mapping and profiling stimulated bioluminescence in the marine environment. *Continental Shelf Research, 3*, 455–464.

Aiken, J., & Williams, R. (1984). Vertical sections of temperature; the UOR. *ICES Oceanographic Data Lists*, *6.1.1*, 5–15.

Aiken, J., Rees, N., Hooker, S., Holligan, P., Bale, A., Robins, D., Moore, G., Harris, R., & Pilgrim, D. (2000). The Atlantic meridional transect: overview and synthesis of data. *Progress in Oceanography*, *45*, 257–312.

Austen, M. C., Buchanan, J. B., Hunt, H. G., Josefson, A. B., & Kendall, M. A. (1991). Comparison of long-term trends in benthic and pelagic communities of the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, *71*, 179–190.

Bainbridge, V., & Cooper, G. A. (1971). Populations of *Sebastes* larvae in the North Atlantic. *Research Bulletin International Commission for the Northwest Atlantic Fisheries*, *8*, 27–35.

Bainbridge, V., & Cooper, G. A. (1973). The distribution and abundance of the larvae of the blue whiting, *Micromesistius poutassou* (Risso), in the North-east Atlantic, 1948–1970. *Bulletins of Marine Ecology*, *8*, 99–114.

Bainbridge, V., & Forsyth, D. C. T. (1972). An ecological survey of a Scottish herring fishery. Part 5: The plankton of the northwestern North Sea in relation to the physical environment and the distribution of herring. *Bulletins of Marine Ecology*, *8*, 21–52.

Bary, B. M. (1964). Temperature, salinity and plankton in the eastern North Atlantic and coastal waters of Britain, 1957. IV. The species relationship to the water body; its role in distribution and in selecting and using indicator species. *Journal of the Fisheries Research Board Canada*, *21*, 183–202.

Batten, S. D., Allen, R. J. S., & Wotton, C. O. M. (1998). The effects of the Sea Empress oil spill on the plankton of the southern Irish Sea. *Marine Pollution Bulletin*, *36*, 764–774.

Batten, S. B., Clark, R., Flinkman, J., Hays, G., John, E., John, A. W. G., Jonas, T., Lindley, A. J., Stevens, D. & Walne, A. (2003). CPR sampling: The technical background, materials and methods, consistency and comparability. *Progress in Oceanography*, this issue, doi:10.1016/j.pocean.2003.08.004.

Batten, S. D., Hirst, A. G., Hunter, J., & Lampitt, R. S. (1999). Mesozooplankton biomass in the Celtic Sea: a first approach to comparing and combining CPR and LHPR data. *Journal of the Marine Biological Association of the United Kingdom*, *79*, 179–181.

Beare, D.J., Batten, S.D., Edwards, M., McKenzie, E., Reid, P.C. & Reid, D.G. (2003). Summarising spatial and temporal information in CPR data. Progress in Oceanography, this issue, doi:10.1016/j.pocean.2003.08.005.

Beare, D. J., & McKenzie, E. (1999a). Continuous Plankton recorder data and diel vertical migration in stage V and VI *Calanus finmarchicus*: a statistical analysis. *Fisheries Oceanography*, *8*, 126–137.

Beare, D. J., & McKenzie, E. (1999b). The multinomial logit model: a new tool for exploring Continuous Plankton data. *Fisheries Oceanography*, *8*, 25–39.

Beare, D. J., & McKenzie, E. (1999c). Temporal patterns in the surface abundance of *Calanus finmarchicus* and *C. helogolandicus* in the North Sea (1958–1966) inferred from Continuous Plankton Recorder data. *Marine Ecology Progress Series*, *190*, 241–251.

Beaugrand, G., & Edwards, E. (2001). Differences in performance among four indices used to evaluate diversity in planktonic ecosystems. *Oceanologica Acta*, *24*, 467–477.

Beaugrand, G., & Ibañez, F. (2002). Spatial dependence of calanoid copepod biodiversity in the North Atlantic Ocean. *Marine Ecology Progress Series*, *232*, 197–211.

Beaugrand, G., Ibañez, F., & Lindley, J. A. (2001). Geographical distribution and seasonal and diel changes in the diversity of calanoid copepods in the North Atlantic and North Sea. *Marine Ecology Progress Series*, *219*, 189–203.

Beaugrand, G., Ibañez, F., Lindley, J. A., & Reid, P. C. (2002a). Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. *Marine Ecology Progress Series*, *232*, 179–195.

Beaugrand, G., Ibañez, F., & Reid, P. C. (2000). Long-term and seasonal fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. *Marine Ecology Progress Series*, *200*, 93–102.

Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A., & Edwards, M. (2002b). Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, *296*, 1692–1694.

Beaugrand, G., Reid, P. C., Ibañez, F., & Planque, B. (2000). Biodiversity of North Atlantic and North Sea calanoid copepods. *Marine Ecology Progress Series*, *204*, 299–303.

Behrenfeld, M. J., Bale, A. J., Kolber, Z. S., Aiken, J., & Falkowski, P. G. (1996). Confirmation of iron limitation of phytoplankton photosynthesis in the equatorial Pacific Ocean. *Nature London*, *383*, 508–511.

Berman, M. S., & Sherman, K. (2001). An undulating towed body sampler for monitoring marine ecosystems. *Sea Technology*, *42*(9), 48–52.

Billett, D. S. M., Lampitt, R. S., Rice, A. L., & Mantoura, R. F. C. (1983). Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature London*, *302*, 520–522.

Bot, P. V. M., van Raaphorst, W., Batten, S., Laane, R., Philippart, K., Radach, G., Frohse, A., Schultz, H., Van den Eynde, D., & Colijn, F. (1996). Comparison of changes in the annual variability of the seasonal cycles of chlorophyll, nutrients and zooplankton at eight locations on the north-west European shelf (1960–1994). *Deutsche Hydrographische Zeitschrift*, *48*, 349–364.

Boyd, P., & Newton, P. (1995). Evidence of the potential influence of planktonic community structure on the interannual variability of particulate organic carbon flux. *Deep-Sea Research, I*, *42*, 619–639.

Brander, K. M. (1992). A re-examination of the relationship between Cod recruitment and *Calanus finmarchicus* in the North Sea. *ICES Marine Science Symposia*, *195*, 393–401.

Brander, K. M., Dickson, R. R. & Edwards, M. (2003). Use of Continuous Plankton Recorder information in support of marine management: Applications in fisheries, environmental protection, and in the study of ecosystem response to environmental change. *Progress in Oceanography*, this issue, doi:10.1016/j.pocean.2003.08.003.

Broekhuizen, N., Heath, M. R., Hay, S. J., & Gurney, W. S. C. (1995). Modelling the dynamics of the North Sea's mesozooplankton. *Netherlands Journal of Sea Research*, *33*, 38–406.

Broekhuizen, N., & McKenzie, E. (1995). Patterns of abundance for *Calanus* and smaller copepods in the North Sea: time series decomposition of two CPR data sets. *Marine Ecology Progress Series*, *118*, 103–120.

Bruce, R. H., & Aiken, J. (1975). The undulating oceanographic recorder—A new instrument system for sampling plankton and recording physical variables in the euphotic zone from a ship underway. *Marine Biology*, *32*, 85–97.

Bryant, A. D., Heath, M., Gurney, W. S. G., Beare, D. J., & Robertson, W. (1997). The seasonal dynamics of *Calanus finmarchicus*: development of a three-dimensional structured population model and application to the northern North Sea. *Journal of Sea Research*, *38*, 361–379.

Buchanan, J. B. (1993). Evidence of benthic pelagic coupling at a station off the Northumberland coast. *Journal of Experimental Marine Biology and Ecology*, *172*, 1–10.

Cannell, M. G. R., Palutikof, J. P., & Sparks, T. H. (Eds.). (1999). *Indicators of climate change in the UK*. London: DETR/CEH.

Clark, R. A. (2000). Long term changes in the North Sea ecosystem. PhD, University of Newcastle upon Tyne, pp. 294.

Clark, R. A., & Frid, C. L. J. (2001). Long-term changes in the North Sea ecosystem. *Environmental Reviews*, *9*, 131–187.

Clark, R. A., Frid, C. L. J., & Batten, S. (2001). A critical comparison of two long-term zooplankton time series from the central-west North Sea. *Journal of Plankton Research*, *23*, 27–29.

Colebrook, J. M. (1960). Continuous Plankton Records: methods of analysis, 1950–1959. *Bulletins of Marine Ecology*, *5*, 51–64.

Colebrook, J. M. (1963). Continuous Plankton Records: annual variations in the abundance of *Calanus finmarchicus*, 1948–1959. *Bulletins of Marine Ecology*, *6*, 17–30.

Colebrook, J. M. (1964). Continuous Plankton Records: a principal components analysis of the geographical distribution of zooplankton. *Bulletins of Marine Ecology*, *6*, 78–100.

Colebrook, J. M. (1965). On the analysis of variation in the plankton, the environment and the fisheries. *Special Publication of the International Commission for North West Atlantic Fisheries*, *6*, 291–302.

Colebrook, J. M. (1966). Continuous Plankton Records: geographical patterns in the annual fluctuations of abundance of some copepods in the North Sea. In H. Barnes (Ed.), *Some contemporary studies in marine science* (pp. 155–161). London: Allen and Unwin.

Colebrook, J. M. (1972a). Changes in the distribution and abundance of zooplankton in the North Sea, 1948–1969. *Symposium of the Zoological Society London*, *29*, 203–212.

Colebrook, J. M. (1972b). Variability in the distribution and abundance of the plankton. *Special Publication of the International Commission for North West Atlantic Fisheries*, *8*, 167–186.

Colebrook, J. M. (1975). The Continuous Plankton Recorder Survey: automatic data processing methods. *Bulletins of Marine Ecology*, *8*, 123–142.

Colebrook, J. M. (1978). Continuous Plankton Records: zooplankton and environment, North-east Atlantic and North Sea, 1948–1975. *Oceanologica Acta*, *1*, 9–23.

Colebrook, J. M. (1979). Continuous Plankton Records: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. *Marine Biology*, *51*, 23–32.

Colebrook, J. M. (1981). Continuous Plankton Records: persistence in time-series of annual means of abundance of zooplankton. *Marine Biology*, *61*, 143–149.

Colebrook, J. M. (1982a). Continuous Plankton Records: persistence in time-series and the population dynamics of *Pseudocalanus elongatus* and *Acartia clausi*. *Marine Biology*, *66*, 289–294.

Colebrook, J. M. (1982b). Continuous plankton records: phytoplankton, zooplankton and environment, North East Atlantic and North Sea, 1958–1980. *Oceanologica Acta*, *5*, 473–480.

Colebrook, J. M. (1982c). Continuous Plankton Records: seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. *Journal of Plankton Research*, *4*, 435–462.

Colebrook, J. M. (1984). Continuous Plankton Records: Relationship between species of phytoplankton and zooplankton in the seasonal cycle. *Marine Biology*, *83*, 313–323.

Colebrook, J. M. (1985a). Continuous Plankton Records: overwintering and annual fluctuations in the abundance of zooplankton. *Marine Biology*, *84*, 261–265.

Colebrook, J. M. (1985b). Sea surface temperature and zooplankton, North Sea 1948 to 1983. *Journal du Conseil International Exploration de la Mer*, *42*, 179–185.

Colebrook, J. M. (1986a). *Continuous Plankton Records: the distribution and standing crop of the plankton of the shelf and ocean to the west of the British Isles*. In Proceedings of the Royal Society of Edinburgh, *88B*. (pp. 221–237).

Colebrook, J. M. (1986b). Environmental influences on long-term variability in marine plankton. *Hydrobiologia*, *142*, 309–325.

Colebrook, J. M. (1991). Continuous Plankton Records: from seasons to decades in the plankton of the North-east Atlantic. In T. Kawasaki, S. Tanaka, Y. Toba, & A. Taniguchi (Eds.), *Long-term variability of pelagic fish populations and their environments* (pp. 29–45). Oxford: Pergamon Press.

Colebrook, J. M., Glover, R. S., & Robinson, G. A. (1961). Continuous Plankton Records: contribution towards a plankton atlas of the North-eastern Atlantic and the North Sea. General introduction. *Bulletins of Marine Ecology*, *5*, 67–80.

Colebrook, J. M., Reid, P. C., & Coombs, S. H. (1978). Continuous Plankton Records: a change in the plankton of the southern North Sea between 1970 and 1972. *Marine Biology*, *45*, 209–213.

Colebrook, J. M., & Robinson, G. A. (1964). Continuous Plankton Records: Annual variations of abundance of plankton, 1948–1960. *Bulletins of Marine Ecology*, *6*, 52–69.

Colebrook, J. M., & Robinson, G. A. (1965). Continuous Plankton Records: seasonal cycles of phytoplankton and copepods in the North-eastern Atlantic and the North Sea. *Bulletins of Marine Ecology*, *6*, 123–139.

Colebrook, J. M., Robinson, G. A., Hunt, H. G., Roskell, J., John, A. W. G., Bottrell, H. H., Lindley, J. A., & Collins, N. R. (1984). Continuous plankton records: A possible reversal in the downward trend in the abundance of the plankton of the North Sea and the Northeast Atlantic. *Journal du Conseil International pour l'Exploration de la Mer*, *41*, 304–306.

Colebrook, J. M., & Taylor, A. H. (1984). Significant time scales of long-term variability in the plankton and the environment. *Rapports et Proces-verbeux des Reunions. Conseil International pour l' Exploration de la Mer*, *183*, 20–26.

Colijn, F. (1998). The temporal variability of plankton and their physico-chemical environment. *ICES Journal of Marine Science*, *55*, 557–561.

Conversi, A., Piontkovski, S., & Hameed, S. (2001). Seasonal and interannual dynamics of *Calanus finmarchicus* in the Gulf of Maine (northeastern US shelf) with reference to the North Atlantic Oscillation. *Deep-Sea Research, II*, *48*, 519–530.

Coombs, S. H. (1975). Continuous plankton records show fluctuations in larval fish abundance during 1948–1972. *Nature London*, *258*, 134–136.

Coombs, S. H. (1980). Continuous Plankton Records: a plankton atlas of the North Atlantic and North Sea. Supplement 5: young fish, 1948–1972. *Bulletins of Marine Ecology*, *8*, 229–281.

Corten, A. (1999). Evidence from plankton for multi-annual variations of Atlantic inflow in the northwestern North Sea. *Journal of Sea Research*, *42*, 191–205.

Corten, A. (2000). A possible adaptation of herring feeding migrations to a change in timing of the *Calanus finmarchicus* season in the eastern North Sea. *ICES Journal of Marine Science*, *57*, 1261–1270.

Corten, A. & Lindley, J. A. (2003). The use of CPR data in fisheries research. *Progress in Oceanography*, this issue, doi:10.1016/j.pocean.2003.08.008.

Craig, R. E. (1960). A note on the dependence of catches on temperature and wind in the Buchan pre-spawning herring fishery. *Journal du Conseil Permanent International pour l'Exploration de la Mer*, *25*, 185–208.

Cushing, D. H. (1984). The gadoid outburst in the North Sea. *Journal du Conseil Permanent International pour l'Exploration de la Mer*, *41*, 159–166.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, *26*, 249–293.

Dickson, R. R. (1995). The natural history of time series. In T. M. Powell, & J. H. Steele (Eds.), *Ecological time series* (pp. 70–98). New York: Chapman and Hall.

Dickson, R. R., Colebrook, J. M., & Svendsen, E. (1992). Recent changes in the summer plankton of the North Sea. *ICES Marine Science Symposia*, *195*, 232–242.

Dickson, R. R., Kelly, P. M., Colebrook, J. M., Wooster, W. S., & Cushing, D. H. (1988). North winds and production in the eastern North Atlantic. *Journal of Plankton Research*, *10*, 151–169.

Dickson, R. R., & Reid, P. C. (1983). Local effects of wind speed and direction on the phytoplankton of the Southern Bight. *Journal of Plankton Research*, *5*, 441–455.

Duarte, C. M., Cebrian, J., & Marba, N. (1992). Uncertainty of detecting sea change. *Nature, London*, *356*, 190.

Duinveld, G. C. A., Lavaleye, M. S. S., Berghuis, E. M., de Wilde, P. A. W. J., van der Weele, J., Kok, A., Batten, S. D., & de Leeuw, J. W. (1997). Patterns of benthic fauna and benthic respiration on the Celtic continental margin in relation to the distribution of phytodetritus. *Internationale Revue der Gesamten Hydrobiologie*, *82*, 395–424.

Edinburgh Oceanographic Laboratory. (1973). Continuous Plankton Records: a plankton atlas of the North Atlantic and the North Sea. *Bulletins of Marine Ecology 7*, 1-174.

Edwards, M., John, A. W. G., Johns, D. G., & Reid, P. C. (2001). Case history and persistence of the non-indigenous diatom *Coscinodiscus wailesii* in the North-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, *81*, 207–211.

Edwards, M., John, A. W. G., Hunt, H. G., & Lindley, J. A. (1999). Exceptional influx of oceanic species into the North Sea late 1997. *Journal of the Marine Biological Association of the United Kingdom*, *79*, 737–739.

Edwards, M., Reid, P. C., & Planque, B. (2001). Long-term and regional variability of phytoplankton biomass in the North East Atlantic (1960–1995). *ICES Journal of Marine Science*, *58*, 39–49.

Fransz, H. G., Colebrook, J. M., Gamble, J. C., & Krause, M. (1991). The zooplankton of the North Sea. *Netherlands Journal of Sea Research*, *28*, 1–52.

Fromentin, J. M., & Planque, B. (1996). *Calanus* and environment in the eastern North Atlantic. 2. Influence of the North Atlantic Oscillation on *Calanus finmarchicus* and *Calanus helgolandicus*. *Marine Ecology Progress Series*, *134*, 111–118.

Gamble, J. C. (1994). Long-term planktonic time series as monitors of marine environmental change. In R. A. Leigh, & A. E. Johnston (Eds.), *Long-term experiments in agriculture and ecological sciences* (pp. 365–386). Wallingford, UK: CAB International.

Gamble, J. C., & Edwards, M. (1996). *GLOBEC-IOC-SAHFOS-MBA Workshop on the analysis of time series with particular reference* *to the Continuous Plankton Recorder Survey. Plymouth, United Kingdom 4–7 May 1993*. In Workshop Report Intergovernmental Oceanographic Commission, 124. (p. 78).

Gieskes, W. W. C. (1971). Ecology of the Cladocera of the North Atlantic and the North Sea, 1960–1967. *Netherlands Journal of Sea Research*, *5*, 342–376.

Gieskes, W. W. C., & Kraay, G. W. (1977). Continuous Plankton Records: changes in the plankton of the North Sea and its eutrophic southern Bight from 1948 to 1975. *Netherlands Journal of Sea Research*, *11*, 334–364.

Glover, R. S. (1953). The Hardy Plankton Indicator and Sampler: a description of the models in use. *Bulletins of Marine Ecology*, *4*, 7–20.

Glover, R. S. (1957). An ecological survey of the drift fishery off the North-east coast of Scotland. Part II: The planktonic environment of the herring. *Bulletins of Marine Ecology*, *5*, 1–43.

Glover, R. S. (1967). The Continuous Plankton Recorder Survey of the North Atlantic. *Symposium of the Zoological Society London*, *19*, 189–210.

Glover, R. S., & Robinson, G. A. (1972). The Continuous Plankton Recorder Survey: plankton around the British Isles during 1970. *Annales Biologique*, *27*, 67–71.

Glover, R. S., Robinson, G. A., & Colebrook, J. M. (1972). Plankton in the North Atlantic—An example of the problems of analysing variability in the environment. In M. Ruivo (Ed.), *Marine pollution and sea life* (pp. 439–445). London: Fishing News Books Ltd.

Halliday, N. C. (1984). Temperature measurements with the Continuous Plankton Recorder in 1981. *Annales Biologique*, *38*, 44–45.

Hardy, A. C. (1923). Notes on the Atlantic plankton taken off the east coast of England in 1921 and 1922. *Publications de Circonstance. Counseil International pour l'Exploration de la mer, Copenhagen*, *78*, 5–10.

Hardy, A. C. (1924). The herring in relation to its animate environment. Pt. I. The food and feeding habits of the herring with special reference to the east coast of England. *Fisheries Investigations, Ser II*, *7*(3), 53.

Hardy, A. C. (1926a). The herring in relation to its animate environment. Pt. II. Report on trials with the Plankton Indicator. *Fisheries Investigations, Ser II*, *8*(7), 13.

Hardy, A. C. (1926b). The Discovery Expedition. A new method of plankton research. *Nature London*, *118*, 630–632.

Hardy, A. C. (1930). *Science and the fishing industry*. Hull: Brown and Sons.

Hardy, A. C. (1935). The Continuous Plankton Recorder. A new method of survey. *Rapports et Proces-verbeux des Reunions. Conseil International pour l' Exploration de la Mer*, *95*, 36–47.

Hardy, A. C. (1936a). Observations on the uneven distribution of oceanic plankton. *Discovery Reports*, *11*, 457–510.

Hardy, A. C. (1936b). The Continuous Plankton Recorder. *Discovery Reports*, *11*, 457–510.

Hardy, A. C. (1939). Ecological investigations with the Continuous Plankton Recorder: object, plan and methods. *Hull Bulletins of Marine Ecology*, *1*, 1–57.

Hardy, A. C. (1956). *The open sea, its natural history. Part I: The world of plankton*. London: Collins pp. 335.

Hardy, A. C. (1959). *The open sea: its natural history. Pt. II. Fish and fisheries, with chapters on whales, turtles and animals of the sea floor*. London: Collins pp. 322.

Hardy, S. A. C. (1967). *Great waters: A voyage of natural history to study whales, plankton and the waters of the Southern Ocean in the old Royal Research Ship Discovery*, with the results brought up to date by the findings of the R.R.S. Discovery II. London: Collins pp. 542.

Hardy, A. C., & Ennis, N. (1936). A test of the validity of the Continuous Plankton Recorder method. *Discovery Reports*, *XI*, 504–509.

Hardy, A. C., Lucas, C. E., Henderson, G. T. D., & Fraser, J. H. (1936). The ecological associations between the herring and the plankton investigated with the plankton indicator. Pt I, II, III & IV. *Journal of the Marine Biological Association of the United Kingdom*, *21*, 147–291.

Hays, G. C. (1995a). Diel vertical migration behaviour of *Calanus hyperboreus* at temperate latitudes. *Marine Ecology Progress Series*, *127*, 301–304.

Hays, G. C. (1995b). Ontogenetic and seasonal variation in the dial vertical migration of the copepods *Metridia lucens* and *Metridia longa*. *Limnology and Oceanography*, *40*, 1461–1465.

Hays, G. C. (1995c). Zooplankton avoidance activity. *Nature London*, *376*, 650.

Hays, G. C. (1996). Large-scale patterns of diel-vertical migration in the North Atlantic. *Deep Sea Research*, *I*, *43*, 1601–1615.

Hays, G. C., Carr, M. R., & Taylor, A. H. (1993). The relationship between Gulf Stream position and copepod abundance derived from the Continuous Plankton Recorder Survey: separating biological signal from sampling noise. *Journal of Plankton Research*, *15*, 1359–1373.

Hays, G. C., Clark, D. R., Walne, A. W., & Warner, A. J. (2001). Large scale patterns of zooplankton abundance in the NE Atlantic in June and July 1996. *Deep-Sea Research*, *II*, *48*, 951–961.

Hays, G. C., Proctor, C. A., John, A. W. G., & Warner, A. J. (1994). Interspecific differences in the diel vertical migration of marine copepods: The implications of size, color, and morphology. *Limnology and Oceanography*, *39*, 1621–1629.

Hays, G. C., Walne, A. W., & Quartley, C. P. (1998). The U-tow: a sysem for sampling mesozooplankton over extended spatial scales. *Journal of Plankton Research*, *20*, 135–144.

Hays, G. C., Warner, A. J., & Lefevre, D. (1996). Long-term changes in the diel vertical migration of the zooplankton. *Marine Ecology Progress Series*, *141*, 149–159.

Hays, G. C., Warner, A. J., & Proctor, C. A. (1995). Spatio-temporal patterns in the diel vertical migration of the copepod *Metridia lucens* in the Northeast Atlantic derived from the Continuous Plankton Recorder Survey. *Limnology and Oceanography*, *40*, 469–475.

Heath, M. R., Backhaus, J. O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn, J., Fraser, J. G., Gallego, A., Hainbucher, D., Hay, S., Jónasdóttir, S., Madden, H., Mardaljevic, J., & Schacht, A. (1999). Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fisheries Oceanograph*, *8*, 163–176.

Heath, M., Scott, B., & Bryant, A. D. (1997). Modelling the growth of herring from four different stocks in the North Sea. *Journal of Sea Research*, *38*, 413–436.

Henderson, G. T. D. (1954). Continuous Plankton Records: the young fish and fish eggs, 1932–39 and 1946–49. *Bulletins of Marine Ecology*, *3*, 215–252.

Henderson, G. T. D. (1957). Continuous Plankton Records: the distribution of young *Gadus poutassou* (Risso). *Bulletins of Marine Ecology*, *4*, 179–202.

Henderson, G. T. D. (1961). Continuous Plankton records: the distribution of young stages of *Sebastes*. *Rapports et Proces-verbeux des Reunions. Conseil International pour l'Exploration de la Mer*, *150*, 216–219.

Hirst, A. G., & Batten, S. D. (1998). Long-term changes in the diel vertical migration behaviour of *Calanus finmarchicus* in the North Sea are unrelated to fish predation. *Marine Ecology Progress Series*, *171*, 307–310.

Hosie, G. W., Fukuchi, M. and Kawaguchi, S. (this volume). Development of the Southern Ocean Continuous Plankton Recorder Survey. *Progress in Oceanography*.

Hunt, H. G. (1968). Continuous Plankton Records: contribution towards a plankton atlas of the north Atlantic and the North Sea. Part XI: The seasonal and annual distributions of Thaliacea. *Bulletins of Marine Ecology*, *6*, 225–249.

Jaschnov, V. A. (1957). The comparative morphology of the species of *Calanus finmarchicus* s. l. *Zoological Journal*, *36*, 191–198.

John, D. D. (1934). The second Antarctic commission of the R.R.S. *Discovery II*. *Geographical Journal*, *83*, 381–398.

John, E. H., Batten, S., Stevens, D., Walne, A. W., Jonas, T., & Hays, G. C. (2002). Continuous plankton records stand the test of time: evaluation of flow rates, clogging and the continuity of the CPR time-series. *Journal of Plankton Research*, *24*, 941–946.

Johns, D. G., Edwards, M., & Batten, S. D. (2001). Arctic boreal plankton species in the North west Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*, 2121–2124.

Joint, I., Wollast, R., Chou, L., Batten, S., Elskens, M., Edwards, E., Hirst, A., Burkill, P., Groom, S., Gibb, S., Miller, A., Hydes, D., Dehairs, F., Antia, A. N., Barlow, R., Rees, A., Pomroy, A., Brockmann, U., Cummings, D., Lampitt, R., Loijens, M., Mantoura, R. F. C., Miller, P., Raabe, T., Salgado, X., Stelfox, C., & Woolfenden, J. (2001). Pelagic production at the Celtic Sea shelf break—the OMEX I project. *Deep-Sea Research, II*, *48*, 3049–3081.

Jossi, J. W., & Goulet, R. R. J. (1993). Zooplankton trends: US north-east shelf ecosystem and adjacent regions differ from North-east Atlantic and North Sea. *ICES Journal of Marine Science*, *50*, 303–313.

Jossi, J. W., John, A. W. G. & Sameoto, D. (2003). Continuous Plankton Recorder sampling off the east coast of North America: history and status. *Progress in Oceanography*, this issue, doi:10.1016/j.pocean.2003.08.010.

Kirby, R. R., & Reid, P. C. (2001). PCR from the CPR offers a historical perspective on marine population ecology. *Journal of the Marine Biological Association of the United Kingdom*, *81*, 539–540.

Landry, M. R., Al-Mutairi, H., Selph, K. E., Christensen, S., & Nunnery, S. (2001). Seasonal patterns of mesozooplankton abundance and biomass at Station ALOHA. *Deep-Sea Research, II*, *48*, 2037–2061.

Lampitt, R. S., & Antia, A. N. (1997). Particle flux in deep seas: regional characteristics and temporal variability. *Deep Sea Research, I*, *44*, 1377–1403.

Le Bureau du Conseil, & Kyle, H. M. (1910). Résumé des observations sur le plankton des mers explorées par le Conseil pendant les années 1902–1908, Première partie. *Bulletin trimestriel des résultats acquis pendant les croisières périodiques et dans les périodes intermédiaires*, Copenhagen: Conseil Permanent International pour l'Exploration de la Mer. i–xxxiv, 1–600.

Lee, C. M. (1971). Population structures of the planktonic copepods *Centropages typicus* and *Temora longicornis* in the North Atlantic area and the functional significance of the reproductive structures of the Centropagidae. PhD thesis, University of Edinburgh, Scotland.

Lee, C. M. (1972). Structure and function of the spermatophore and its coupling device in the Centropagidae (Copepoda: Calanoida). *Bulletins of Marine Ecology*, *8*, 1–20.

Levitus, S., Antonov, J. I., Wang, J., Delworth, T. L., Dixon, K. W., & Broccoli, A. J. (2001). Anthropogenic warming of Earth's climate system. *Science*, *292*, 267–270.

Licandro, P., Conversi, A., Ibañez, F., & Jossi, J. (2001). Time series analysis of interrupted long-term data set (1961–1991) of zooplankton abundance in Gulf of Maine (northern Atlantic, USA). *Oceanologica Acta*, *24*, 453–466.

Lindley, J. A. (1975). Continuous Plankton Records: a plankton atlas of the North Atlantic and the North Sea. Supplement 3: Tintinnida (Protozoa, Ciliophora) in 1965. *Bulletins of Marine Ecology*, *8*, 201–213.

Lindley, J. A. (1977). Continuous Plankton Records: the distribution of the Euphausiacea (Crustacea: Malacostraca) in the North Atlantic and the North Sea, 1966–67. *Journal of Biogeography*, *4*, 121–133.

Lindley, J. A. (1982). Population dynamics and production of euphausiids. 3. *Meganyctiphanes norvegica* and *Nyctiphanes couchi* in the North Atlantic Ocean and the North Sea. *Marine Biology*, *66*, 37–46.

Lindley, J. A. (1987). Continuous Plankton Records: the geographical distribution and seasonal cycles of decapod crustacean larvae and pelagic post-larvae in the North-eastern Atlantic Ocean and the North Sea, 1981–3. *Journal of the Marine Biological Association of the United Kingdom*, *67*, 145–167.

Lindley, J. A. (1988). Estimating biomass and production of pelagic larvae of brachyuran decapods in western European shelf waters. *Journal of Experimental Marine Biology and Ecology*, *122*, 195–211.

Lindley, J. A. (1997). Eggs and their incubation as factors in the ecology of planktonic crustacea. *Journal of Crustacean Biology*, *17*, 569–576.

Lindley, J. A. (1998). Diversity, biomass and production of decapod crustacean larvae in a changing environment. *Invertebrate Reproduction and Development*, *33*, 209–219.

Lindley, J. A., & Batten, S. D. (2002). Long-term variability in the diversity of North Sea zooplankton. *Journal of the Marine Biological Association of the United Kingdom*, *82*, 31–40.

Lindley, J. A., Gamble, J. C., & Hunt, H. G. (1995). A change in the zooplankton of the central North Sea (55° to 58°N): a possible consequence of changes in the benthos. *Marine Ecology Progress Series*, *119*, 299–303.

Lindley, J. A., & Hunt, H. G. (1989). The distributions of *Labidocera wollastoni* and *Centropages hamatus* in the North Atlantic Ocean and the North Sea in relation to the role of resting eggs in the sediment. In J. S. Ryland, & P. A. Tyler (Eds.), *Reproduction, genetics and distributions of marine organisms* (pp. 407–413). Fredensborg: Olsen & Olsen.

Lindley, J. A., Roskell, J., Warner, A. J., Halliday, N., Hunt, H. G., John, A. W. G., & Jonas, T. (1990). Doliolids in the German Bight in 1989: evidence for exceptional inflow into the North Sea. *Journal of the Marine Biological Association of the United Kingdom*, *70*, 679–682.

Lindley, J. A., & Williams, R. (1980). Plankton of the Fladen Ground during FLEX 76. II. Population dynamics and production of *Thysanoessa inermis* (Crustacea: Euphausiacea). *Marine Biology*, *57*, 79–86.

Lindley, J. A., & Williams, R. (1994). Relating plankton assemblages to environmental variables using instruments towed by ships-of-opportunity. *Marine Ecology Progress Series*, *107*, 245–262.

Lindley, J. A., & Reid, P. C. (2002). Variations in the abundance of *Centropages typicus* and *Calanus helgolandicus* in the North Sea: deviations from close relationships with temperature. *Marine Biology*, *141*, 153–165.

Lindley, J. A., Reid, P. C., & Brander, K. (2003). Inverse relationship between cod recruitment in the North Sea and young fish in the Continuous Plankton Recorder Survey. *Scientia Marina*, *67*(Suppl. 1), 191–200.

Longhurst, A. (1998). *Ecological geography of the sea*. London: Academic Press pp. 398.

Longhurst, A. R., & Williams, R. (1976). Improved filtration systems for multiple-serial plankton samplers and their deployment. *Deep Sea Research*, *23*, 1067–1073.

Lucas, C. E. (1940). Ecological investigations with the Continuous Plankton Recorder: the phytoplankton in the southern North Sea 1932–1937. *Hull Bulletins of Marine Ecology*, *1*, 73–170.

Lucas, C. E. (1941). Continuous Plankton Records: phytoplankton in the North Sea 1938–1939. Part I: Diatoms. *Hull Bulletins of Marine Ecology*, *2*, 19–46.

Lucas, C. E. (1942). Continuous Plankton Records: phytoplankton in the North Sea 1938–1939. Part II: Dinoflagellates. *Hull Bulletins of Marine Ecology*, *2*, 47–70.

Lucas, C. E., & Stubbings, H. G. (1948). Continuous Plankton Records: size variations in diatoms and their ecological significance. *Hull Bulletins of Marine Ecology*, *2*, 133–171.

Madin, L. P., Horgan, E. F., & Steinberg, D. K. (2001). Zooplankton at the Bermuda Atlantic Time-series Study (BATS) station: Seasonal and interannual variation in biomass 1994–1998. *Deep-Sea Research, II*, *48*, 2063–2082.

Matthews, J. B. L. (1966). Experimental investigations of the systematic status of *Calanus finmarchicus* and *Calanus glacialis* (Crustacea: Copepoda). In H. Barnes (Ed.), *Some contemporary studies in marine science* (pp. 479–492). London: George Allen & Unwin Ltd.

Matthews, J. B. L. (1967). *Calanus finmarchicus* s.l. in the North Atlantic. The relationship between *Calanus finmarchicus* s.str., *C. glacialis* and *C. helgolandicus*. *Bulletins of Marine Ecology*, *6*, 159–179.

Mills, D. K., Walne, A., Reid, P. C., & Heaney, S. I. (1998). Updating the Continuous Plankton Recorder: an improved tool for integrated plankton monitoring. *ICES Journal of Marine Science*, *55*, 814–817.

Myers, R. A., Barrowman, N. J., Mertz, G., Gamble, J., & Hunt, H. G. (1994). Analysis of Continuous Plankton Recorder Data in the Northwest Atlantic 1959–1992. *Canadian Technical Report of Fisheries and Aquatic Sciences 1966*, iii + pp. 249.

North Sea Task Force (1993). North Sea Quality Status Report 1993. London: Oslo and Paris Commissions; Fredensborg, Denmark: Olsen & Olsen, vi + pp. 132.

Olson, T. A., Odlaug, T. O., & Swain, W. R. (1966). The Continuous Plankton Recorder—a review of the literature. *University of Minnesota Water Research Centre Bulletin*, *3*, vii.

Owens, N. J. P., Cook, D., Colebrook, M., Hunt, H. G., & Reid, P. C. (1989). Long term trends in the occurrence of *Phaeocystis* sp. in the North-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom, 69*, 813–821.

OSPAR Commission (2000). Quality Status Report 2000, Region III—Celtic Seas. London: OSPAR Commission, pp. 116.

Pingree, R. D., & Griffiths, D. K. (1978). Tidal fronts on the shelf seas around the British Isles. *Journal of Geophysical. Research (Oceans and Atmospheres)*, *83*, 4615–4622.

Planque, B., & Batten, S. D. (2000). *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. *ICES Journal of Marine Science*, *57*, 1528–1535.

Planque, B., & Fromentin, J. M. (1996). *Calanus* and environment in the eastern North Atlantic. 1. Spatial and temporal patterns of *C. finmarchicus* and *C. helogolandicus*. *Marine Ecology Progress Series*, *134*, 101–109.

Planque, B., Hays, G. C., Ibañez, F., & Gamble, J. C. (1997). Large scale spatial variations in the seasonal abundance of *Calanus finmarchicus*. *Deep-Sea Research, I*, *44*, 315–326.

Planque, B., & Reid, P. C. (1998). Predicting *Calanus finmarchicus* abundance from a climatic signal. *Journal of the Marine Biological Association of the United Kingdom*, *78*, 1015–1018.

Planque, B., & Taylor, A. H. (1998). Long-term changes in zooplankton and the climate of the North Atlantic. *ICES Journal of Marine Science*, *55*, 644–654.

Radach, G. (1984). Variations in the plankton in relation to climate. *Rapports et Proces-verbeux des Reunions. Conseil International pour l'Exploration de la Mer*, *185*, 234–254.

Radach, G., Gekeler, J., Bot, P., Castaing, P., Colijn, F., Damm, P., Danielssen, D. F. L., Gamble, J. C., Laane, R., Mommaerts, J. P., Nehring, D., Pegler, K., van Raaphorst, W., & Wilson, J. (1996). The NOWESP research database. *Deutsche Hydrographische Zeitschrift*, *48*, 241–259.

Rae, K. M. (1952). Continuous Plankton Records: explanation and methods, 1946–1949. *Hull Bulletins of Marine Ecology*, *3*, 135–155.

Rae, K. M., & Fraser, J. H. (1941). Ecological investigations with the Continuous Plankton Recorder: the Copepoda of the southern North Sea, 1932–1937. *Hull Bulletins of Marine Ecology*, *1*, 171–238.

Rae, K. M., & Rees, C. B. (1947). Continuous Plankton Records: the Copepoda in the North Sea, 1938–1939. *Hull Bulletins of Marine Ecolog,y*, *2*, 95–134.

Rebstock, G. A. (2001). Long-term stability of species composition in calanoid copepods off southern California. *Marine Ecology Progress Series*, *215*, 213–224.

Rees, C. B. (1949). Continuous Plankton Records: the distribution of *Calanus finmarchicus* (Gunn.) and its two forms in the North Sea, 1938–1939. *Hull Bulletins of Marine Ecology*, *2*, 215–275.

Rees, C. B. (1950). The identification and classification of lamellibranch larvae. *Bulletins of Marine Ecology*, *3*, 73–104.

Rees, C. B. (1951). Continuous Plankton Records: first report on the distribution of lamellibranch larvae in the North Sea. *Bulletins of Marine Ecology*, *3*, 105–134.

Rees, C. B. (1952). Continuous Plankton Records: the decapod larvae in the North Sea, 1947–1949. *Bulletins of Marine Ecology*, *3*, 157–184.

Rees, C. B. (1957). Continuous Plankton Records: the distribution of *Calanus finmarchicus* (Gunn.) in the North Sea and the North-eastern Atlantic, 1946–1953. *Bulletins of Marine Ecology*, *4*, 211–246.

Reid, P. C. (1975). Continuous Plankton Records: large scale changes in the abundance of phytoplankton in the North Sea from 1958-1973. International Council for the Exploration of the Sea, CM 1975/L:7, 12 pp. (mimeo).

Reid, P. C. (1978a). Continuous Plankton Records: large scale changes in the abundance of phytoplankton in the North Sea from 1958–1973. *Rapports et Proces-verbeux des Reunions. Conseil International pour l'Exploration de la Mer*, *172*, 384–389.

Reid, P. C. (1978b). Dinoflagellate cysts in the plankton. *New Phytology*, *80*, 219–229.

Reid, P. C. (1984). Year-to-year changes in zooplankton biomass, fish yield and fish stock in the North Sea. International Council for the Exploration of the Sea, CM 1984/L:39, 7 pp.

Reid, P. C. (1999). What are the principles for managing ocean ecosystems? In E. Maltby, M. Holdgate, M. Acreman, & A. G. Weir (Eds.), *Ecosystem management: questions for science and society* (pp. 93–102). Egham, UK: Royal Holloway, University of London.

Reid, P. C., & Hunt, H. G. (1998). Are observed changes in the plankton of the North Atlantic and North Sea linked to climate change? In Proceedings of the Second International Conference on Pelagic Biogeography, vol. 142. *Intergovernmental Oceanographic Commission Workshop Report* (pp. 310–315).

Reid, P. C., & John, A. W. G. (1978). Tintinnid cysts. *Journal of the Marine Biological Association of the United Kingdom*, *58*, 551–557.

Reid, P. C., & Edwards, M. (2001). Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senckenbergiana Maritima*, *31*, 107–115.

Reid, P. C., Robinson, G. A., & Hunt, H. G. (1987). Spatial and temporal patterns of marine blooms in the North-eastern Atlantic and North Sea from the Continuous Plankton Recorder Survey. *Rapports et Proces-verbeux des Reunions. Counseil International pour l'Exploration de le Mer*, *187*, 27–37.

Reid, P. C., Lancelot, C., Gieskes, W. W. C., Hagmeier, E., & Weichart, G. (1990). Phytoplankton of the North Sea and its dynamics: A review. *Netherlands Journal of Sea Research*, *26*, 295–331.

Reid, P. C., Surey-Gent, S. C., Hunt, H. G., & Durrant, A. E. (1992). *Thalassiothrix longissima*, a possible oceanic indicator species in the North Sea. *ICES Marine Science Symposia*, *195*, 268–277.

Reid, P. C., Edwards, M., Hunt, H. G., & Warner, A. J. (1998a). Phytoplankton change in the North Atlantic. *Nature London*, *391*, 546.

Reid, P. C., Planque, B., & Edwards, M. (1998b). Is observed variability in the long-term results of the Continuous Plankton Recorder survey a response to climate change? *Fisheries Oceanography*, *7*, 282–288.

Reid, P. C., Battle, E. J., Batten, S. D., & Brander, K. M. (2000). Impacts of fisheries on plankton community structure. *ICES Journal of Marine Science*, *57*, 495–502.

Reid, P. C., de Borges, M. F., & Svendsen, E. (2001a). A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fisheries Research*, *50*, 163–171.

Reid, P. C., Holliday, N. P., & Smyth, T. J. (2001b). Pulses in the eastern margin current and warmer water off the north west European shelf linked to North Sea ecosystem changes. *Marine Ecology Progress Series*, *215*, 283–287.

Robertson, A. (1968). Abundance, distribution, and biology of plankton in Lake Michigan with the addition of a research ships of opportunity project. Great Lakes Research Division, Institute of Science and Technology, University of Michigan, Special Report, No. 35, pp. 43.

Robinson, G. A. (1965). Continuous Plankton Records: Contribution towards a plankton atlas of the North Atlantic and the North Sea. Part IX: Seasonal cycles of phytoplankton. *Bulletins of Marine Ecology*, *6*, 104–122.

Robinson, G. A. (1970). Continuous Plankton Records: variation in the seasonal cycle of phytoplankton in the North Atlantic. *Bulletins of Marine Ecology*, *6*, 333–345.

Robinson, G. A., Aiken, J., & Hunt, H. G. (1986). Synoptic surveys of the western English Channel. The relationships between plankton and hydrography. *Journal of the Marine Biological Association of the United Kingdom*, *66*, 201–218.

Robinson, G. A., Budd, T. D., John, A. W. G., & Reid, P. C. (1980). *Coscinodiscus nobilis* (Grunow) in Continuous Plankton Records, 1977–1978. *Journal of the Marine Biological Association of the United Kingdom*, *60*, 675–680.

Robinson, G. A., & Hiby, A. R. (1978). The Continuous Plankton Recorder Survey. In A. Sournia (Ed.), *Phytoplankton Manual* (pp. 59–63). Paris: UNESCO.

Rothschild, B. A. (1998). Year class strengths of zooplankton in the North Sea and their relation to cod and herring abundance. *Journal of Plankton Research*, *20*, 1721–1741.

Rozwadowski, H. M. (2002). *The sea knows no boundaries: a century of marine science under ICES*. Seattle & London: University of Washington Press pp. 448.

Sameoto, D. (2001). Decadal changes in phytoplankton color index and selected Calanoid copepods in Continuous Plankton Recorder data from the Scotian Shelf. *Canadian Journal of Fisheries and Aquatic Science*, *58*, 749–761.

Sars, G. O. (1903). An account of the Crustacea of Norway. 4, Bergen, pp. 171 .

Sims, D. W., & Reid, P. C. (2002). Congruent trends in long-term zooplankton decline in the North-east Atlantic and basking shark (*Cetorhinus maximus*) fishery catches off west Ireland. *Fisheries Oceanography*, *11*, 59–63.

Shermann, K. (1994). Sustainability, biomass yields, and health of coastal ecosystems: an ecological perspective. *Marine Ecology Progress Series*, *112*, 227–301.

Shermann, K., & Duda, A. M. (1999). An ecosystem approach to global assessment and management of coastal waters. *Marine Ecology Progress Series*, *190*, 271–287.

Stephens, J. A., Jordan, M. B., Taylor, A. H., & Proctor, R. (1998). The effects of fluctuations in North Sea flows on zooplankton abundance. *Journal of Plankton Research*, *20*, 943–956.

Stevens, D., & Reid, P. C. (in press). History of the Continuous Plankton Recorder Survey. Intergovernmental Oceanographic Commission, Special publication, Proceedings, The colour of ocean data.

Taylor, A. H. (1995). North-south shifts of the Gulf Stream and their climatic connection with the abundance of zooplankton in the UK and its surrounding seas. *ICES Journal of Marine Science*, *52*, 711–721.

Taylor, A. H., Allen, J. I., & Clark, P. A. (2002). Extraction of a weak climatic signal by an ecosystem. *Nature, London*, *416*, 629–632.

Taylor, A. H., & Stephens, J. A. (1980). Latitudinal displacements of the Gulf Stream (1966 to 1977) and their relation to changes in temperature and zooplankton abundance in the N.E. Atlantic. *Oceanologica Acta*, *3*, 145–149.

The Continuous Plankton Recorder Survey Team (1992). Continuous plankton records: the North Sea in the 1980s. *ICES Marine Science Symposia*, 195, 243–248.

UNCED (1992). Earth Summit, http://habitat.igc.org/agenda21.

Verheye, H. M., & Richardson, A. J. (1998). Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951–1996): bottom-up or top-down control? *ICES Journal of Marine Science*, *55*, 803–807.

Vezzulli, L., & Reid, P. C. (2003). The CPR survey (1948–1997) a gridded database browser of plankton abundance in the North Sea. *Progress in Oceanography*, this issue, doi:10.1016/j.pocean.2003.08.011.

Warner, A. J., & Hays, G. C. (1994). Sampling by the Continuous Plankton Recorder survey. *Progress in Oceanography*, *34*, 237–256.

Williams, R. (1975). Continuous Plankton Records: a plankton atlas of the North Atlantic and North Sea. Supplement 4: The ostracoda in 1963. *Bulletins of Marine Ecology*, *8*, 215–228.

Williams, R. (1988). Spatial heterogeneity and niche differentiation in oceanic zooplankton. *Hydrobiologia*, *167/168*, 151–159.

Williams, R., & Aiken, J. (1990). Optical measurements from underwater towed vehicles deployed from ships-of-opportunity in the North Sea. *Environment and Pollution Measurement Sensors and Systems*, *1269*, 186–194.

Williams, R., & Lindley, J. A. (1980). Plankton of the Fladen Ground during FLEX 76. III. Vertical distribution, population dynamics and production of *Calanus finmarchicus* (Crustacea: Copepoda). *Marine Biology*, *60*, 47–56.

Williams, R., & Lindley, J. A. (1982). Variability in abundance, vertical distribution and ontogenetic migrations of *Thysanoessa longicaudata* (Crustacea: Euphausiacea) in the North-eastern Atlantic Ocean. *Marine Biology, 69*, 321–330.

Williams, R., & Lindley, J. A., (1992). Factors determining plankton abundance in the North Sea. Final Contract Report to Department of the Environment. Ref: 7/8/121. Plymouth Marine Laboratory. 1–44.

Williams, R., & Lindley, J. A. (1998). Strategy and application for sampling large marine ecosystems with the Continuous Plankton Recorder and undulating oceanographic recorder/aquashuttle. In K. Sherman, E. N. Okemwa, & M. J. Ntiba (Eds.), *Large marine ecosystems of the Indian Ocean: assessment, sustainability and management* (pp. 45–60). Oxford: Blackwell Science.

Williams, R., & Robins, D. (1981). Seasonal variability in abundance and vertical distribution of *Parathemisto gaudichaudi* (Amphipoda: Hyperiidea) in the North east Atlantic Ocean. *Marine Ecology Progress Series*, *4*, 289–298.

Williams, R., Lindley, J. A., Hunt, H. G., & Collins, N. R. (1993). Plankton community structure and geographical distribution in the North Sea. *Journal of Experimental Marine Biology and Ecology*, *172*, 143–156.

Williamson, M. H. (1961). An ecological survey of a Scottish Herring fishery. Part IV: Changes in the plankton during the period 1949–1959. *Bulletins of Marine Ecology, 5*, 207–229.

Zeitzschel, B. (1965). The distribution of tintinnids in the North Atlantic Ocean. International Council for the Exploration of the Sea, CM 1965/L:12, pp. 6 (mimeo).