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The use of CPR data in fisheries research

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Abstract

The Continuous Plankton Recorder (CPR) survey was initiated partly to contribute to our understanding of the variability of fish stocks and as a potential method for predicting fish distributions from the abundance and composition of the plankton. The latter objective has been superseded by technological developments in fish detection, but the former has been the subject of continuing, and in recent years expanding use of the CPR data. Examples are presented of application of the data to studies on North Sea herring, cod, mackerel, blue whiting and redfish as well as more general plankton studies relevant to fisheries research. Variations in the migration patterns of herring as well as recruitment have been related to abundances and species composition of the plankton in the CPR survey. Extensive use has been made of the CPR data in relation to cod, particularly in the development and testing of the 'match-mismatch' hypothesis. Advection of sufficient numbers of *Calanus* from the core oceanic areas of its distribution into the areas where the cod stocks occur may partly determine the success of those stocks. The analysis of the distribution and abundances of mackerel larvae in the CPR survey have shown contrasting variations between the North Sea and Celtic Sea. The expansion of the horse mackerel fishery in the north-eastern North Sea since 1987 has been related to physical events and a 'regime shift' in the plankton, described from CPR data. The oceanic spawning areas of the blue whiting and redfish were highlighted by the expansion of the CPR survey into the north-eastern and north-western Atlantic respectively. These results helped to focus the attention of fisheries scientists on stocks that have subsequently become the targets for commercial exploitation. The results of the CPR survey, particularly those on *Calanus finmarchicus*, the phytoplankton standing stock as measured by the CPR colour index, the overall patterns of trends in plankton abundance and distributions of indicator species have been used by fisheries scientists to interpret variations in fish stocks. Generally the CPR data can be used to determine whether changes in the distributions and growth rates of fish have resulted from changes in planktonic food, changes in strength of ocean currents and distribution of water masses and to identify trends in larval abundances. With the tightening regulation of fisheries to reduce overfishing, global climate change and changing anthropogenic inputs into the sea, the unique source of information on unexploited populations in the long-term time series of the CPR survey will be of increasing value to fisheries scientists in the study of natural variability.

Keywords: Fisheries; Plankton; Monitoring; Variability; Climate; North Atlantic; North Sea

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Contents

1. Introduction

One of the original objectives of the CPR survey was to improve our understanding of the natural fluctuations in commercial fish stocks (Hardy, 1939). It is appropriate, therefore, to consider the various ways in which the CPR survey has been contributing to our knowledge of the relationship between plankton and fisheries. However, this topic is wide ranging as fish and plankton are so closely related that almost any study on plankton has some relevance to fisheries research. Even if not all the plankton data seemed relevant at the time of collection, subsequently some have turned out to be important in a historical perspective. To restrict the subject of this review to manageable proportions, it was decided to focus attention on those plankton studies that have had a demonstrable effect on fisheries research. This arbitrary selection, means that many studies on, for instance, the distribution of larvae of commercial species, have been omitted (e.g. Hart, 1974). Also, this review will not consider the effects of fisheries on plankton (e.g. Lindley, Gamble and Hunt (1995), Reid, Battle, Batten, & Brander, 2000). On the other hand, it will include some studies that were not primarily directed at commercial fish species, but have nevertheless contributed to our understanding of their fluctuations.

Two of the original objectives of the Survey were to benefit the fishing industry by predicting fish distributions and to describe and explain the natural fluctuations in the fisheries. Advances in fish finding technology have rendered the first objective redundant, but the use of CPR data continues to describe and explain natural variability. In the following two sections, results from a number of studies will be presented that illustrate the practical value of CPR data to fisheries research. The first section presents studies dealing directly with commercial fish species. The second section outlines a number of studies that were primarily aimed at plankton species, but have had important implications for fisheries research. This review concludes with a general discussion of the potential and limitations of CPR data to fisheries research, and possible future applications.

2. Historical development of the relationship between the CPR survey and fisheries research

When the CPR survey was launched, one of the main objectives was to obtain a better understanding of the fluctuations of commercial fisheries. Hardy (1939) wrote: “The present survey was conceived as a means of studying the broad changes taking place in the plankton distribution of the North Sea and their relation to the changing hydrological and meteorological conditions on the one hand, and with fluctuations in the fisheries on the other”. Hardy had been intrigued by the relationship between fish and plankton from the early days of his career as a marine scientist. He was appointed in 1921 at the Fisheries Laboratory in Lowestoft to study the feeding habits of the herring and its relations to the plankton in general. Hardy (1956) described how in the autumn of his first year in Lowestoft, he went out on a herring drifter, taking his plankton net along. The catches were poor. The skipper ascribed these disappointing catches to the occurrence of “weedy water” or “Dutchman’s baccy juice” (water distinctly coloured by phytoplankton). So Hardy set out to test the validity of the skipper’s hypothesis that there was an inverse relationship between herring catches and phytoplankton. He developed a small plankton sampler called the ‘plankton indicator’ that could be deployed from commercial fishing boats (Hardy, 1926). In 1922 and 1923, fishing skippers were asked to deploy this instrument prior to shooting their nets. The initial results confirmed there was a striking negative relationship between herring catches and phytoplankton. From then onwards, Hardy was convinced of the value of monitoring plankton to improve understanding of the variability of the distribution of commercial fish. He wrote “The study of these (plankton) changes has always held a particular attraction for me: surely no-one can doubt that here must lie important keys to a better understanding of success or failure in the fisheries” (Hardy, 1956).

The development of the CPR was a follow-up to these experiments with the plankton indicator. Hardy was aware of the patchy nature of plankton distributions, and he realised that in order to understand fully the fluctuations in the fisheries, he had to know the large-scale pattern in plankton variation. To quote his words again: “The changes of fortunes in the fisheries, apart from those brought about by man’s own folly in overfishing, must have their causes in the natural world; the relation between cause and effect, however, will only be understood when we have an unbroken record of the changes in the sea month by month over a very wide area for very many years” (Hardy, 1956). The CPR was designed to collect precisely that kind of information.

Hardy had hoped that the understanding of the relationship between plankton and fisheries would ultimately enable fisheries scientists to use real-time plankton information to help fishermen in the same way as meteorological information was used to help farmers. He wrote in 1956: “It is now possible to forecast the weather a day or two in advance; since ocean currents move so much more slowly than the streams of air, it is likely that, given comparable information, we will in time be able to forecast events in the sea a week or two ahead—long enough to be of value in guiding fishing boats to more economic fishing”. Following this approach, the Lowestoft Laboratory had started to issue plankton reports to herring fishermen before World War II. These reports were broadcast over the radio in order to help fishermen avoid areas of phytoplankton concentration and so to increase their herring catches.

The CPR programme originally held two promises of practical application to fisheries: the prediction of fish (herring) distribution to fishermen in real time, and a better understanding by scientists of the natural fluctuations in the stocks. However, the introduction of new electronic fish finding equipment and the subsequent depletion of many (pelagic) fish stocks in the fisheries between 1950 and 1980 made both fishermen and fishery scientists turn their attention away from plankton.

For fishermen, the use of plankton had only been an indirect method of locating fish concentrations. Therefore, their interest in plankton disappeared as soon as direct methods of locating the fish, the echo sounder and sonar, became generally available. These instruments had been developed for anti-submarine warfare during World War II, and could indicate the position, depth, and quantity of the target species. Sonar technology continued to improve so that swaths of at least 2 km on both sides of the vessel could be scanned. With such powerful fish finding technologies, the fishing skippers no longer needed the plankton indicators.

The introduction of electronic fish finding equipment sharply increased the efficiency of fishing. Its development coincided with another technical breakthrough: the invention of the Puretic power block for purse seine fishing. Both innovations contributed to sharp increases in the effectiveness of fishing, particularly on pelagic stocks, and increased fishing mortality among these stocks. Within only 20 years, all the main pelagic fish stocks in Western European waters were severely depleted, in some cases to the verge of commercial extinction. The fisheries for Norwegian spring spawning herring, North Sea herring, Celtic Sea herring and Scottish west coast herring had to be closed completely for several years in the late 1970s and early 1980s to enable the stocks to recover. These rapid declines in the commercial fish stocks through overfishing focused the attention of fisheries research almost exclusively on man-induced effects to the neglect of natural variations in the stocks and their underlying environmental causes. Most of the fishery scientists that started work on pelagic stocks in the 1970s and 1980s had high expectations of population and ecosystem modelling. They ascribed to the belief that changes in fish stocks would eventually be understood by using mathematical models that described the relationships between the fisheries and the stocks, and the interactions between the various stocks. The expansion of computational power dramatically increased the capacity for mathematical modelling, and further encouraged this development. In this conceptual world of static, mechanistic ecosystems, many fishery scientists considered that there was no role for unpredictable, natural variations. This was not conducive to the continuation of studies on natural variations in plankton and fish stocks.

However, the interest in natural variability was re-kindled after 1980, a milestone being the publication of Cushing's (1982) book 'Climate and fisheries'. After the extension of economic zones in Western Europe in 1977, the possibilities for conservation had increased and fishery managers had started to implement the advice of fisheries scientists. However, it soon became apparent that the stocks were not behaving according to the predictions from population models, and scientists were forced to conclude that fishing was not the only significant factor affecting the stocks of mackerel (Walsh & Martin, 1986), herring (Corten, 1986), sandeels (Bailey, 1989) and sprat (Bakken & Bailey, 1990). Attention to natural changes in fish stocks was also revived by a symposium on long-term changes in marine fish populations held in Vigo (Wyatt & Larrañeta, 1988).

However, most of the fisheries scientists engaged in stock assessments in Western Europe had not been involved in plankton research and largely remained ignorant about its implications. It was some years before they 'discovered' that an important plankton monitoring system had existed for many decades, and that the data collected under this programme could provide valuable clues as to the causes of the natural fluctuations in fish stocks.

3. Use of CPR data in studies on commercial fish species

Examples are presented of the outcomes of studies in which CPR data were used in direct connection with commercial fish species; this review is not comprehensive and reflects the personal interests of the authors. These studies were conducted either by fishery scientists who used CPR data in their analyses, or by plankton experts that provided information on the distribution of commercial species.

3.1. North Sea herring (Clupea harengus)

As outlined above in section 2, Hardy's original interest in the relationships between plankton and fisheries was in connection with the herring fishery. Herring is a plankton feeder, so it was expected that the fish's distributions and abundances would be strongly influenced by the distribution of plankton, so

CPR data would be of direct value in helping to understand why the fish are found only in certain areas. An example of the relationship between herring and its planktonic food based on CPR data was published by Corten (2000). This study addressed the unusual distribution of herring catches in the North Sea in the first years after the reopening of the herring fishery in 1983. In the years prior to the fishing ban (1977–1983), catches in early summer used to be taken in the western North Sea, whereas during the first years after the reopening the main catches were taken in the eastern part. That area is where the herring overwinter and the fish normally stay until May, before migrating westwards. The high catches in early summer in the eastern area post-1983 suggested that the herring had postponed their westward migration, possibly because feeding conditions had improved in the eastern North Sea. An analysis of CPR data showed that this was indeed the case.

During the years 1976–1984, the main food organism of the herring, *Calanus finmarchicus*, remained abundant in the eastern North Sea until June or July (Fig. 1), whereas normally the abundance of this copepod declines after May (Planque & Fromentin, 1996). The herring had apparently adapted their migrations to this change in timing of the *Calanus* season, postponing their departure to the western North Sea until July. After 1984, the *Calanus* season in the eastern North Sea once again shortened and the herring migrated westwards earlier. From 1990 onwards, the bulk of the catches in June again originated from the western North Sea.

During 1988–1990 there was another event probably indicating the influence of the plankton on the distribution of North Sea herring. In the summers of these years the herring migrated further north than

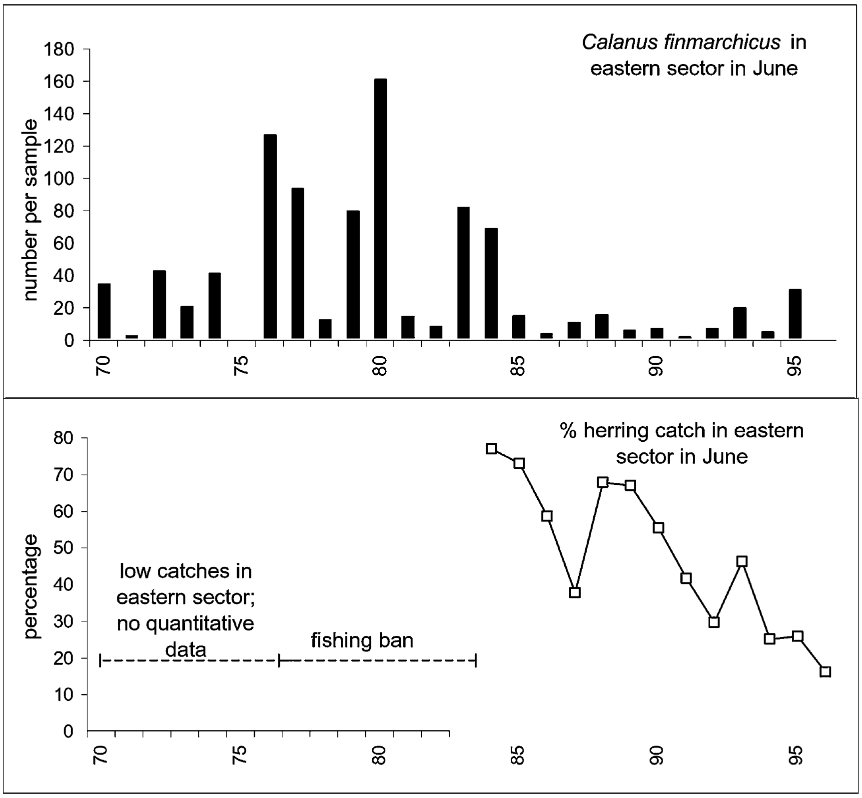

Fig. 1. Abundance of *Calanus finmarchicus* in June in the north-eastern North Sea (top figure) compared with the percentage of the total North Sea herring catch taken in the eastern sector during the same month (lower figure). From Corten, 2001b.

usual, possibly even as far as Faeroese waters (Jacobsen, 1990). The years 1988–1990 were characterised by an extreme, positive phase of the North Atlantic Oscillation (NAO), and an accompanying strong westerly circulation during winter (Corten, 2001a). Planque and Fromentin (1996) and Fromentin and Planque (1996) have shown that there is an inverse relationship between the NAO index and the abundance of *C. finmarchicus* in the North Sea. In years when the NAO index is high, not only does the abundance of *C. finmarchicus* decline in the North Sea, but also the centre of its distribution shifts to the north. This is probably because the species has a boreal distribution, and is poorly adapted to the relatively high winter and spring temperatures that occur during a positive phase of the NAO. The northern shift in the distribution of *C. finmarchicus*, during the strong positive NAO phase in 1988–1990, probably resulted in the northwards extension of the feeding migrations of North Sea herring during those years.

Apart from providing information on the feeding environment for the herring, CPR data can be used to identify water masses, and thereby help to understand changes in the herring distributions that are caused by long-term variations in ocean currents. Glover (1955, 1957) compared the distribution of herring catches in the north-western North Sea with plankton data obtained by the Plankton Indicator. He found there had been a southward shift in the herring fishery in 1947 to 1953, associated with an increase in occurrence of oceanic plankton. He concluded that “some characteristic of oceanic water may have arrived in the North Sea in greater quantity and it may have moved southwards at a progressively earlier date”, and that this increase in oceanic influence was the cause of the southward shift in the herring fishery. Bainbridge and Forsyth (1972) and Bainbridge, Forsyth and Canning (1978), again comparing herring catches with data from the Plankton Indicator, found an opposite trend after 1955. The herring catches shifted north, while the abundance of its favoured planktonic food (*Calanus* and Spiratella) on the southern grounds off Aberdeen declined. They concluded that variations in the distribution of planktonic food (and thereby of herring catches) were largely determined by variations of the Atlantic inflow. This was again taken up by Corten (1999a) who investigated the cause of the recruitment failure of herring in the 1970s. In these years, herring larvae resulting from spawning in the north-western North Sea no longer reached the nursery areas in the eastern half of the North Sea, apparently because their transport by the residual currents had reduced. Corten used CPR data to test the hypothesis that long-term fluctuations in the Atlantic inflow into the north-western North Sea were the cause of these changes in the transport of the herring larvae. He examined data for the temporal variations of twenty species of Atlantic plankton in the north-western North Sea during 1948–1996. These twenty species could be divided into four groups, each with distinctive biological characteristics. One group containing *Candacia armata* and *Metridia lucens* proved to be the best indicator of variations of Atlantic inflow. Each year the species in this group are advected into the North Sea by the inflow of Atlantic water, where they survive for several months; long enough to be used as tracers of Atlantic water. This group of species underwent a long-term variation, with peaks in their abundance around 1960 and 1990, and a trough from 1964 to 1980 (Fig. 2). These plankton data confirmed that there was a sustained reduction of Atlantic inflow in the 1960s and 1970s, which was probably the cause of the failure of herring recruitment during those years. In another study Corten (1999b) used the long-term variation of Atlantic inflow to explain the disappearance of spawning herring off Aberdeen in 1965 to 1983.

3.2. Cod (Gadus morhua)

CPR data have been used to follow the long-term changes in the stocks of North Sea cod. Cod and other gadoid species underwent a spectacular expansion in the North Sea during the early 1960s; an event often referred to as the ‘gadoid outburst’ (Cushing, 1975, 1984). A great deal of research effort was expended trying to understand the causes underlying this sudden and dramatic expansion. One of the more plausible explanations was Cushing’s (1984) ‘match-mismatch hypothesis. Based on CPR data, it was shown that there had been a delay in the onset of the *Calanus finmarchicus* season in the north-eastern North Sea during 1962–1978. *C. finmarchicus* is the dominant zooplankton species in this area during the

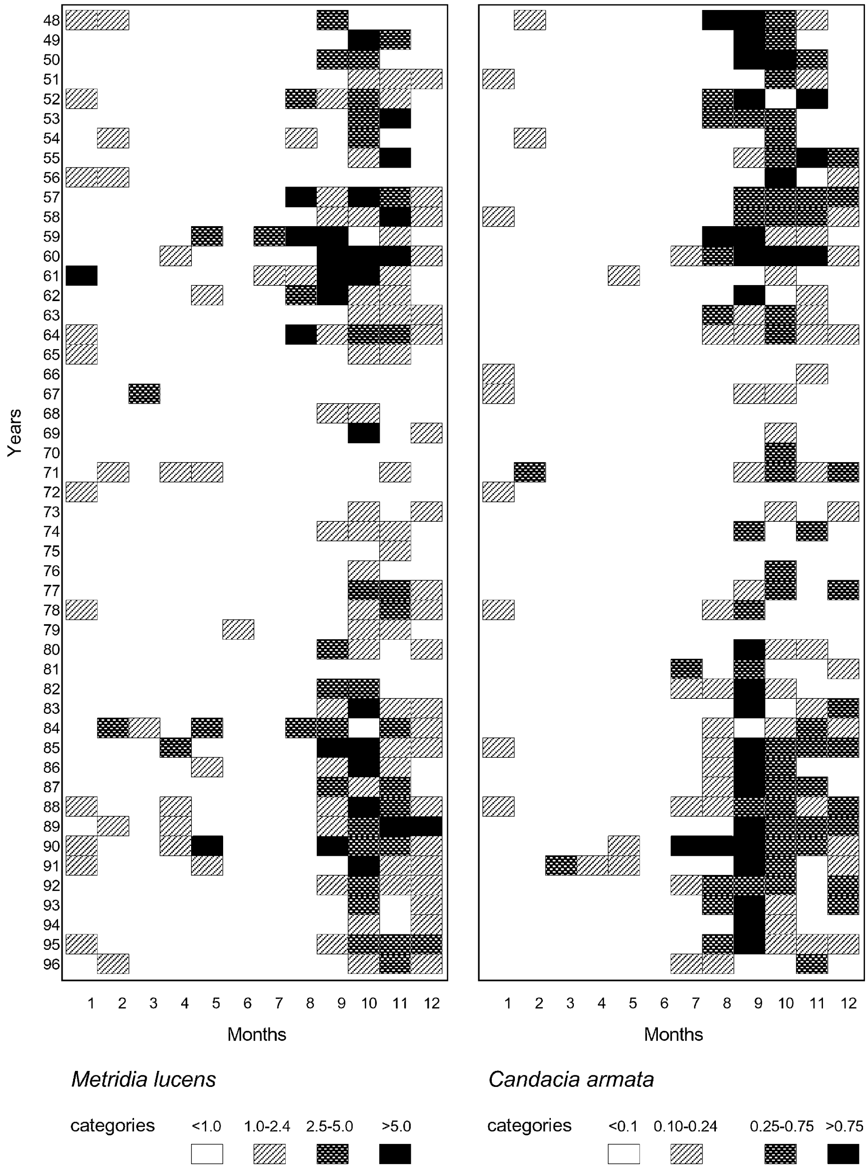

Fig. 2. Long-term variations in the abundance of two planktonic indicators for Atlantic water in the north-western North Sea. From Corten, 1999a.

first half of the year (Fransz, Colebrook, Gamble, & Krause, 1991) and the main food item for many juvenile fish, including cod. Cushing suggested that the delay in the onset of the *C. finmarchicus* season improved the synchronisation between the development of juvenile cod (born in February) and the abundance of their staple food, and this resulted in better survival and growth of the juvenile cod.

Cushing's explanation has been questioned latterly, notably by Brander (1992) who compared the recruitment of cod and timing of the *Calanus* season for the period 1962–1986, instead of the period 1954–1977 used by Cushing. He found no significant correlation, but admitted that the model he used was probably incomplete, since it treated the whole North Sea cod stock as a single unit dependent on the abundance of copepods in only one part of the North Sea. In the 1970s and 1980s especially, a large portion of the new cod year-classes grew up in the German Bight area, an area, which was not included in Brander's analysis of food supply. Although Brander suggested that Cushing's relationship between cod and *Calanus* is not universally applicable, the match-mismatch hypothesis remains one of the more plausible explanations for the gadoid outburst in the North Sea during the 1960s.

Rothschild (1994) pointed to the synchrony between the general decline of cod stocks in the North Atlantic since the 1960s, and the decline of biological productivity as indicated by the CPR data for phytoplankton and zooplankton. He suggested that not only are there long-term trends in ocean productivity but also that they are a major cause of variations in commercial fish stocks. Later Rothschild (1998) showed that a large year-class of *Calanus* or *Para/Pseudocalanus* was one of the requirements for a strong cod year-class.

Sundby (2000) looked at long-term variations in cod recruitment in the various stocks around the periphery of the North Atlantic. All these stocks are found around the centre of distribution of *C. finmarchicus*, which is in the middle of the North Atlantic. Sundby speculated that recruitment success in any of these cod populations was partly dependent on the sufficient advection of *Calanus* from its central high-density area to the peripheral areas where the cod occur. This advection depends on large-scale oceanic processes, and hence is partly related to the North Atlantic Oscillation.

Lindley, Reid and Brander (2003) analyse a highly significant negative relationship between cod recruitment and the numbers of young fish (mainly Clupeidae and Ammodytidae) in the CPR survey in the North Sea. Their results indicate that either the stocks of clupeids and sandeels have a significant trophic interaction with cod or that the numbers of the young fish in the CPR integrate the influence of several climatic variables with effects on cod recruitment, which are counter to those favouring clupeid and ammodytid spawning. Taylor, Allen and Clarke (2002) have demonstrated that correlations between the Gulf Stream North Wall Index and zooplankton in the North Sea are also probably the result of a similar integration of climatic variables linked to the position of the Gulf Stream.

Coombs (1980) observed that young cod were found in CPR samples from the German Bight near Helgoland in the years 1948–1956, but were absent in later years. The cod's spawning area had apparently shifted to the Southern Bight between Holland and the English coast. The years 1948–1954 were characterised by an increased spawning in the North Sea of species of fish normally associated with warmer waters, such as anchovy, horse mackerel, pilchard and sole (Aurich, 1953, 1958). Cod recruitment in the North Sea is inversely related to temperature (O'Brien, Fox, Planque, & Case, 2000). Hence the German Bight, with its lower temperatures during the spawning period (February), may have been providing a more suitable spawning area than the Southern Bight when conditions had improved for the warmer water species.

3.3. Mackerel (Scomber scombrus)

Results from the CPR survey have been used to describe long-term trends in the distribution and abundance of mackerel larvae in the North Sea and to the south and west of the British Isles (Bainbridge, Cooper, & Hart, 1974; Coombs & Mitchell, 1981). So far, these results have not yet been used to examine changes in the mackerel stocks, despite their potential in this respect.

In the late 1960s, pronounced changes took place in the mackerel stock in the North Sea. The large stock that used to spawn and overwinter in the North Sea was reduced by heavy fishing during autumn and winter. By the end of the 1960s it had virtually ceased to exist, and most scientists attributed this decline of the stock solely to overfishing. However, Postuma (1972) showed that recruitment to the North Sea population began to decline after 1958, long before the period of overexploitation. Apparently, the increase in fishing pressure coincided with the impact of some natural change that was leading to a decline in the stock. Shortly after the mackerel had disappeared from the North Sea, heavy concentrations of overwintering mackerel were found to have appeared in the English Channel off Cornwall. These concentrations were a new phenomenon, suggesting there had been a natural increase in the mackerel stock west of the British Isles (Lockwood, 1988).

The data presented by Coombs and Mitchell (1981) provided additional information on the long-term trends in the mackerel stocks in the North Sea and to the south of the British Isles. They show that the abundances of mackerel larvae in the North Sea were low in 1948–1956 but increased in subsequent years. It is possible that the increase in mackerel spawning in the North Sea around 1960 was related to the increase in inflow of water with an oceanic influence that was indicated in the CPR data for *Candacia* and *Metridia* (Fig. 2). In the Celtic Sea, there was a reduction in the numbers of mackerel larvae in the early 1960s, which coincided with the increases in abundance in the North Sea. The CPR data on mackerel larvae in the North and Celtic Seas thus show there were long-term and inverse fluctuations in their abundance, suggesting some kind of interaction. There may even have been exchanges between the spawning stocks in the North Sea and in the Celtic Sea in response to long-term environmental variations.

Inverse fluctuations between populations in the North Sea and Celtic Sea, in response to long-term environmental variations, have also been reported for the copepod *Centropages typicus* (Reid & Planque, 2000). This species is near the northern limits of its distribution in the CPR area (like the mackerel), and its abundance was found to correlate positively with the NAO in the North Sea, but negatively in the Celtic Sea.

3.4. Horse mackerel (Trachurus trachurus)

After 1987, a new and important fishery for horse mackerel developed in the north-eastern North Sea. These horse mackerel belonged to the western stock, whose population spawns in spring in the Celtic Sea and feeds in summer to the west of the British Isles and in the northern North Sea. This expansion of the fishery in the North Sea probably stemmed from an increase in the immigration of western horse mackerel. Several explanations have been offered for this immigration, including the result of an increase in stock size following the very strong 1982 year-class, and higher water temperatures. Reid, Borges and Svendsen (2001) showed that the increase in landings of western horse mackerel in the North Sea coincided with an increase in the Phytoplankton Colour index of the CPR samples; they considered these and associated changes to be evidence of a 'regime shift' in the area. The cause of the shift may have been an increase in the inflow of Atlantic water, as suggested by the simulations of the NORWECOM hydrodynamic model, and the concomitant increased nutrient input.

3.5. Blue whiting (Micromesistius poutassou)

Henderson (1953) reported the first records of blue whiting larvae in CPR samples from oceanic waters to the west of Britain in the period 1946–1949. As CPR sampling was extended further into the oceanic areas of the Northeast Atlantic, blue whiting became the subject of several further studies, which established the seasonal cycles and changes in the abundance of larvae and the geographical extent of the spawning areas (Henderson, 1953, 1957, 1961a). The demonstration of enormous spawning concentrations of blue whiting to the west of the British Isles by the CPR survey was one of the factors that raised the interest of fisheries biologists in this species (Bainbridge & Cooper, 1973). As a result, in 1967 the Marine Laboratory Aberdeen initiated a programme of exploratory trawling together with intensive surveys of fish eggs and larvae to assess the potential of blue whiting as the basis for an industrial fishery (Raitt, 1968; Bailey & Seaton, 1969; Bailey, 1970). This contributed to the development of a fishery that yielded catches in excess of 1,000,000 tonnes per year in 1998–2000 (Anon, 2001). The distribution of blue whiting larvae in the CPR survey is shown by the square symbols in Fig. 3.

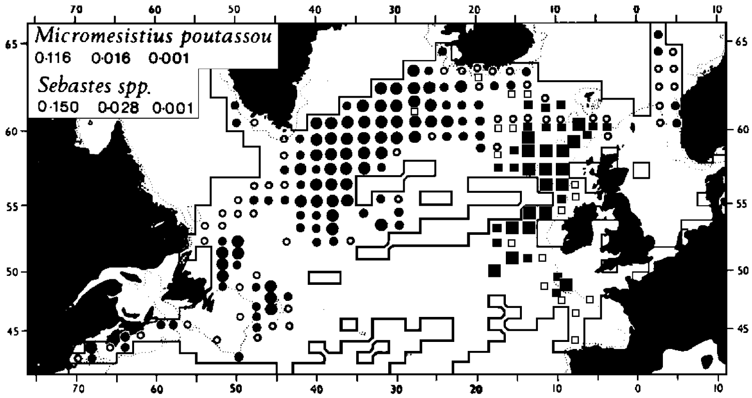

Fig. 3. The distributions of blue whiting (*Micromesistius poutassou*, square symbols) and redfish (*Sebastes* spp., circles) from Coombs (1980). The numbers in the top left show the numbers per sample indicated by the large filled symbols, medium divided symbols and small open symbols respectively.

3.6. Redfish (Sebastes mentella)

After the extension of the CPR survey to Ocean Weather Station Alfa in 1955 and south-westward from Iceland from 1957 onwards, larvae of *Sebastes spp.* were found abundantly in CPR samples from the Irminger Sea. The distribution of these larvae in the northern Atlantic was charted and the specific identities of the stocks were determined (Henderson, 1961b, 1961c, 1964, 1965; Bainbridge, 1965; Bainbridge & Cooper, 1971; Roskell, 1986). As in the case of blue whiting, the CPR results helped to focus the attention of fisheries scientists on the oceanic stocks of redfish, and their research led to the development of a commercial fishery; during the 1990s the annual catch in the Irminger Sea exceeding 100,000 tonnes (Anon, 2001). The distribution of the larvae of the Sebastes species in the CPR survey is shown by the circles in Fig. 3.

4. Plankton studies with relevance to fisheries research

Studies aimed primarily at phyto- and zooplankton have often produced information of direct relevance to fisheries research. Firstly, plankton is important, either directly or indirectly, as food for the fish. Secondly, the plankton composition in an area provides information on the type and history of water and the integrated effects of currents in an area that directly affect fish distributions. We now cite some examples of plankton studies that have directly influenced fisheries research.

4.1. Studies on Calanus finmarchicus

Calanus finmarchicus is the dominant zooplankton species in the North Atlantic, and the species has been the subject of intensive research, much of which was based on CPR data. Because the species is a major food item of several commercial fish species (herring, blue whiting, mackerel, juvenile cod), changes in its abundance or distribution can affect their recruitment, growth and distribution.

Cushing, 1966, 1982, 1983, 1984) extensively studied CPR data on *Calanus finmarchicus* with the aim of understanding changes in the North Sea ecosystem. Some of his findings have already been mentioned above in section 3.2. Stephens, Jordan, Taylor and Proctor (1998) related *Calanus* abundance in various parts of the North Sea to water transport. Planque and Fromentin (1996) and Fromentin and Planque (1996) used CPR data to investigate the distribution and abundance of *C. finmarchicus* in the north-eastern Atlantic in relation to environmental conditions. They found that the abundance of the copepod was negatively correlated with temperature, and that in years following mild winters the distribution of species contracted to the north. The abundance of the species was negatively correlated with the NAO-index. These findings have been used to explain changes in commercial fish stocks, such as herring (Corten, 1999b) and cod (Sundby, 2000).

4.2. Phytoplankton colour

Phytoplankton Colour, measured from CPR samples, provides an index both of the timing and intensity of primary production. Although the relationship between phytoplankton and fish is less direct than in the case of zooplankton, the phytoplankton index may provide a proxy for the timing and volume of food production.

Brander and Dickson (1984) used CPR data on phytoplankton colour to investigate why the fish production is lower in the Irish Sea than in the North Sea. They found that the phytoplankton maximum develops later in the Irish Sea than in the North Sea, which they attributed to the intensity of tidal streaming limiting the area of seasonally stratified water and delaying the onset of stratification. The Irish Sea resembles the western area of the southern Bight in the North Sea, which is also characterised by strong tidal streams.

Reid, Borges and Svendsen (2001) used the Phytoplankton Colour index for the northern North Sea as an indication of the amount of food that would ultimately be available to the fish (and particularly the horse mackerel) in this area.

4.3. Trends in total phytoplankton and zooplankton

CPR data have been used demonstrate the long-term trends in total phyto- and zooplankton standing crops in the north-eastern Atlantic (e.g. see Colebrook, 1978; Colebrook, Robinson, Hunt, Roskell, John, Bottrell et al., 1984; Dickson, Kelly, Colebrook, Wooster, & Cushing, 1986; Reid & Edwards, 2002). Although these trends will not be reflected immediately in the abundances of each fish species in every part of the region, eventually changes in the overall characteristics of biological production will sooner or later affect most, if not all, commercial fish stocks. Aebisher, Coulson and Colebrook (1990) drew attention to the synchrony between developments in phytoplankton, zooplankton, fish and birds in the western North Sea in the period 1950–1990. Rothschild (1994) considered the declining trend in total phyto- and zooplankton in CPR samples from the north-eastern Atlantic as evidence for a general decline in biological productivity in this area, which he proposed was a feasible explanation for the general decline of the region's cod stocks. Reid and Planque (2000) also explored the effects of climatic variation on long-term trends in the phytoplankton and zooplankton in describing and analysing the marine environment of the North Atlantic stocks of salmon.

4.4. Plankton indicator species

Each plankton species has different preferences with regards to its abiotic environment, and consequently each water mass is characterised by a specific combination of plankton species (Colebrook, 1972; Beaugrand, Ibañez, Lindley, & Reid, 2002). The plankton composition in a particular area thus allows conclusions to be drawn about the origins and environmental history of the water, additional to those that can be drawn from purely physico-chemical data. Extending this study over a number of years shows the degree of inter-annual hydrographic variation, which may also affect commercial fish stocks.

Many reports based on CPR data have described variations of Atlantic influence in the northern North

Sea. Examples are Rae (1956); Fraser (1969), and the annual reports to Annales Biologiques (e.g. Glover & Robinson, 1965). CPR data on plankton indicator species were also used by Corten (1999a) to investigate long-term variations of Atlantic inflow into the North Sea. His findings were used to explain changes in herring recruitment, and shifts in herring spawning areas in the north-western North Sea (section 3.1). Variations of Atlantic inflow into the North Sea are also likely to have had consequences for other commercial species in the area.

5. Discussion

5.1. Applications of CPR data in fisheries research

We have cited several examples of how CPR data have been useful in clarifying and sometimes resolving problems encountered by fisheries scientists. CPR results have proved to be useful in the following situations:

(a) Changes in the distributions or recruitment to fish stocks often implicate changes in food distribution or abundance. In those stocks for which the diet is planktonic, the CPR data provides directly relevant information to test the hypotheses based on changes in quantity, quality, timing and availability of food supply.
(b) Fluctuations in the distributions of both juvenile and adult fish often imply the importance of changes in the strength of currents and/or the distributions of water masses. When hydrographic data are unavailable, because there are no current meter observations or interpretations of the physico-chemical properties of the water are ambiguous, the use of plankton indicator species may enable assessments of these changes. Persistent plankton species can be used as ‘tags’ for the different water masses, indicating the origin of certain water masses, even after warming, cooling, or mixing with other types of water have modified its physical and chemical properties. However, large numbers of species are recorded in the CPR survey, showing many different patterns of variation, so if the selection of species present is arbitrary and limited, the evidence of the water’s history may be misleading. The correct procedure is to make an *a priori* selection of a number of plankton organisms based on their ecological characteristics, and see whether this subgroup exhibits the patterns expected on the basis of the postulated hypothesis.
(c) Uncertainty exists as to the size and distribution of spawning populations in earlier years. In this case, CPR data can give a rough indication (depending on the area coverage) of long-term trends in larval distribution and abundance. This information may be used to establish the existence of long-term natural variability in certain stocks.

5.2. Limitations of CPR data

The CPR survey was not designed to address specific fisheries problems, but to monitor fluctuations in plankton populations over wide geographical areas and over long time periods. The survey, therefore, necessarily has a low resolution and should not be used to address problems at small temporal and spatial scales.

In practice, this means that CPR data can rarely be used to monitor small year-to-year changes in stock size on the basis of the abundance of fish eggs or larvae. In cases where stock assessment of commercial species depends on an estimate of spawning products, dedicated surveys have to be initiated with a far finer resolution in time and space than the CPR survey. Examples are the co-ordinated herring larvae surveys in the North Sea of the International Council for the Exploration of the Sea (ICES), and mackerel and horse mackerel egg surveys in the Celtic Sea. However, the CPR data can place these fine scale studies in a large time and space frame.

In recent years the number of transects that are sampled regularly has had to be reduced because of budget restrictions. The number of transects in the North Sea was severely reduced after 1985, and for some parts of the North Sea the sampling coverage is now insufficient to use CPR data for an analysis of local trends in plankton composition. However, Sameoto (2001), working on CPR data from the American continental shelf, has shown that useful information about changes in plankton communities can sometimes be derived despite gaps in the time series.

Finally it should be noted that, like all plankton samplers the CPR records only a limited segment of the full size range of the planktonic communities. In particular it is a poor sampler of phytoplankton. The silk mesh is far too coarse to retain quantitatively anything other than large chain-forming species, and although these are a large part of the total spring flora over mid- and high latitude continental shelfs, during other seasons and in offshore regions they are minor constituents. So data on ‘total phytoplankton’ have to be interpreted with caution.

5.3. New applications of CPR data

During 1960–2000 fisheries scientists were pre-occupied with fishery-induced effects on the stocks. They made relatively little use of CPR data and showed little interest in the natural variability of the ecosystem. Even so, during the last two decades, management of most commercial fish stocks in the areas covered by the CPR survey has been considerably improved. This has led to the rebuilding of several stocks, sometimes in a spectacular way (Norwegian spring spawning herring), that were in serious trouble in the 1960s and 1970s. Under the new management regimes, fisheries managers are now attempting to stabilise yields by fixing fishing mortality rates at a low and constant level, in the expectation that both the stocks and the fisheries will stabilise.

However, once the impact of fishing mortality on the stocks has been reduced, the role of natural variability will become relatively more important. Even under a regime of constant, low fishing mortality, stocks will continue to fluctuate in response to variations in the environment. There is a fundamental need for fisheries scientists to be more aware of natural variability, because if they do not understand it and its underlying causes, they will be unable to separate fisheries impacts from natural variations, which will compromise the effectiveness of their conservation measures. A growing interest in natural fluctuations in the fish stocks will increase the requirement for long-term data series of environmental parameters. The CPR database is virtually the only existing source of information on long-term and large-scale changes in inshore and oceanic ecosystems.

An important current field of interest is the prediction of environmental responses to the changes in global climates resulting from increasing greenhouse gas concentrations in the atmosphere. It is now fashionable to ascribe any new variation in fish stocks to global climate change, even when there is no evidence for changes in the temperature regime. CPR data can be of great value in evaluating whether present changes in the ecosystem are indeed a new development, or whether they are part of the normal variability of the system. With more than 50 years of information available in computerised format, the CPR dataset is one of very few sources of appropriate time series suited to assess natural variability.

The study of changes in fish stocks that may have occurred as a result of variations of anthropogenic nutrient input into the sea is a possible further application of CPR data. As an example, greatly increased growth of most commercial fish species in the southern North Sea in the 1950s and 1960s was attributed to the increased input of industrially produced nitrate and phosphate (Boddeke & Hagel, 1995; Nanninga, Gieskes, & Wolff, 1997). An agreement between the North Sea states on limiting nutrient inputs into the North Sea has resulted in a drastic reduction in phosphate discharges by the coastal states from 1985. This reduction has been followed by a decline in growth rates in several commercial fish species in the southern

North Sea (Boddeke & Hagel, 1995; Nanninga, Gieskes & Wolff, 1997). There is currently a debate as to whether these declines in growth rates in fish in the southern North Sea are either a direct effect of the decreased phosphate emissions or the result of other factors. An analysis of long-term trends in the abundance of planktonic food, based on CPR data, may help to resolve the real cause of the reduced fish production in this area.

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