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What we have learned about plankton variability and its physical controls from 70 years of CPR records

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The first tow of the Continuous Plankton Recorder (CPR) Survey took place in September 1931 between Hull and Hamburg in the North Sea. The development of the CPR was, for Sir Alister Hardy, one contribution to the "great plan" of ICES, the ultimate aim of which was "the rational exploitation of the sea". Seven decades and 200 000 samples later, the survey is the longest plankton monitoring programme ever carried out and is now a major player in biological oceanography research in the North Atlantic. From the description of plankton species in the early days of the survey, the knowledge gained from the CPR has evolved to spatial distribution, seasonal dynamics, interannual and interdecadal variability, responses of populations to climatic forcing, and changes in the ecosystem structure and dynamics. The building of the CPR plankton series, which has paralleled the initiation and maintenance of monitoring programmes by ICES, has provided support and interpretative power to the many environmental and biological data series collected under the auspices of the Council. These data series now form the basis of our understanding of the North Atlantic ecosystem over the scale of greatest variability: the multi-decadal scale.

Keywords: climate variability, Continuous Plankton Recorder, ecosystem changes, long-term changes, North Atlantic, seasonal changes.

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Introduction

In 1926, on his return from the "Discovery" expedition, Alister Hardy presented a "new method of plankton research" (Kemp, 1926) and described the first model of the Continuous Plankton Recorder (CPR-Type 1). The objective was to design "an instrument which, by giving a continuous record mile by mile to scale, would 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-netting whether any correlation exists between different species". Hardy later improved CPR-Type 1 (Figure 1b) used in the "Discovery" expedition into a smaller and easy-to-handle CPR-Type 2 (Figure 1c), making it possible to tow the CPR with non-research vessels. This change in technology was the critical step towards the development of a large-scale plankton survey, the aims of which are "attempting to apply methods similar to those employed in meteorolo-

gy to a study of the changing plankton distribution, its causes and effects" (Hardy, 1939a).

Inspired by his first trials with the plankton indicator (Figure 1a) to help fishermen in their search for herring schools, Hardy also saw in the CPR an important instrument to help the fishing industry. The "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 the fluctuations in the fisheries on the other." Investigations from the CPR survey were directly linked to fisheries and were part of ICES' great plan for a "rational exploitation of the sea" (Hardy, 1939b).

In summary, Hardy's CPR survey had three principal objectives: 1) to improve the ways of sampling plankton and to measure its variability in time and space, 2) to develop adequate techniques so that advances in plankton biology would benefit fisheries, and 3) to relate plankton changes to hydroclimatic variability. The present paper concentrates on the latter objective and attempts

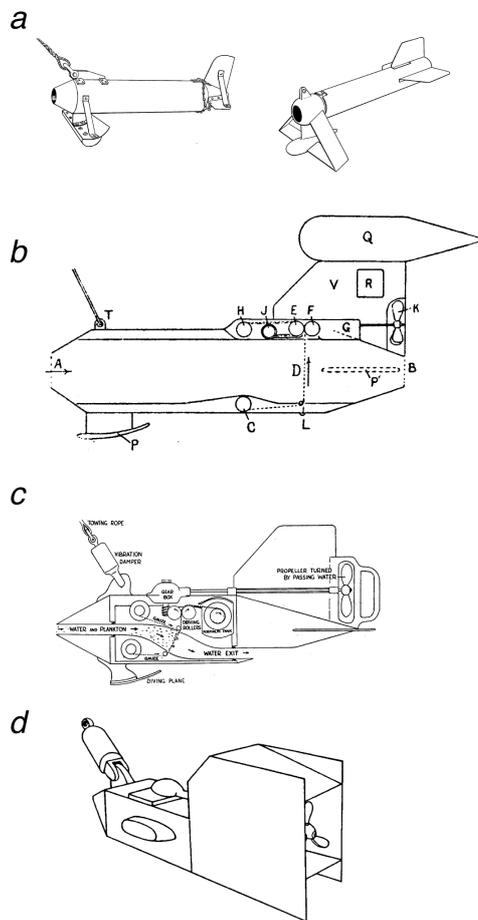


Figure 1. The Plankton Recorders: (a) two models of Hardy's Plankton Indicator, reproduced from Glover (1953), (b) the Continuous Plankton Recorder-Type 1, used on the "Discovery" expedition, reproduced from Hardy (1926), (c) the Continuous Plankton Recorder-Type 2, used in the CPR survey from 1931 to 1986, reproduced from Hardy (1939a), and (d) the present Continuous Plankton Recorder-Type 2, fitted with the box-tail, first used in the CPR survey in 1975, reproduced from Hays and Warner (Hays and Warner, 1993). Instruments are not represented to scale.

to summarize the achievements of the CPR survey in describing plankton variability and its relationship to physical forcing from its start in the early 1930s to the present.

Spatial distribution of plankton

The cartography of the spatial distribution of plankton was part of the objectives of the survey from the beginning of Hardy's work. From 1939 to 1973, most of the CPR was devoted to the cartography of plankton in the ocean in a way similar to that of meteorological clima-

tologies. In 1940, Lucas provided the first reports on the ecological study of the phytoplankton changes carried out as part of the new CPR survey. In this work, the changes in phytoplankton distribution in time and space were studied along three CPR "lines" across the southern North Sea, and the spatial analysis was restricted to a series of uni-dimensional comparisons along the CPR tow routes. Despite its simplicity, this method quickly revealed the large-scale patterns in the distribution of the diatoms *Rhizosolenia styliformis*, *Biddulphia sinensis*, and the flagellate *Phaeocystis*, three taxa thought to be of particular importance to the herring fishery (see Hardy, 1925). Similar work followed on a number of taxa, while the number of CPR routes increased and the series of data got longer (see *Hull Bulletins of Marine Ecology*, Volumes 1–4).

In 1958, in parallel with the development of computing technology J. M. Colebrook developed a new method for the mapping of CPR records in two dimensions, based on the aggregation of data in squares of 2° longitude \times 2° latitude grid (Colebrook, 1961). This radical change in the spatial representation of the data allowed for the direct comparison of the changes in spatial distribution of single taxa over time or of the variations in spatial patterns across taxa. The standardized cartographic technique was used to prepare a plankton atlas of the North Atlantic and the North Sea, which was published in 1973 (Oceanographic Laboratory of Edinburgh, 1973), shortly followed by a number of supplementary volumes concerned with additional specific taxa. This was the first atlas of plankton distribution of that scale, and it is a "true" climatology based on several years or several decades of data. Today, there is still no equivalent to the CPR Atlas for other regions of the world ocean. The approach of Colebrook has enabled the construction of plankton maps comparable to those of climate or hydrography, and since the first application in 1961, a large number of research articles have been devoted to the comparative studies of the plankton and its environment, using this original technique.

Recently, alternative cartographic methods have been applied in replacement of Colebrook's 1958 averaging technique. The geostatistical method of kriging was used in a series of contributions (e.g., Planque and Fromentin, 1996; Planque, *et al.*, 1997; Planque and Ibanez, 1997), and techniques designed to produce estimates of abundance using combined spatial and temporal information have been proposed by Beare and McKenzie (1999). Methods for the cartography of multispecific data have also been developed and used successfully by Williams *et al.* (1993) and Colebrook (1964, 1972), amongst others.

Seasonal changes

The first results of the survey were concerned with the seasonality of phytoplankton (Lucas, 1940) and zoo-

plankton (Rae and Fraser, 1941). The accumulation of data over large areas and for a number of years has provided an immense set of data with which to test hypotheses concerning the seasonal control of primary and secondary production. The hypothesis of Gran and Braarud (1935), later demonstrated by Riley (1942) and Sverdrup (1953) on the control of primary production through light intensity and water column stratification, was discussed by Colebrook and Robinson (1961). Using CPR data, Colebrook and Robinson observed that the timing and duration of phytoplankton production was markedly different between the North Sea and areas of the western European shelf, and they attributed these dissimilarities to differences in the development of stratification in the two areas. Later, Robinson (1965) and Colebrook and Robinson (1965) confirmed the distinct seasonal dynamics of phytoplankton in the North Sea and off-shelf areas, and reported a similar geographical division when they considered the seasonality of copepod abundance recorded by the CPR. The analysis was further extended to the entire North Atlantic when sufficient data became available (Robinson, 1970). In this later work, Robinson provided the first set of large-scale empirical evidence for the link between the timing of onset of phytoplankton blooms and the development of stratification in the North Atlantic. The control of phytoplankton production via stratification has been re-examined and discussed many times since the works of Robinson and Colebrook (e.g., Townsend *et al.*, 1992, 1994). The addition of results from more recent studies has reinforced the general view that wind and solar radiation during the winter-spring period are the critical factors determining the timing and amplitude of phytoplankton blooms at mid-latitudes, even though phytoplankton production sometimes develops without apparent stratification (Townsend *et al.*, 1992). Results from the CPR survey have provided one of the best examples of changes in timing and duration of phytoplankton blooms in the Northeast Atlantic. These are most likely a direct response to climatic influence in this region (Figure 2) (Reid, 1975; Dickson and Reid, 1983; Reid *et al.*, 1987; Dickson *et al.*, 1988; Reid *et al.*, 1998).

An analysis similar to that of Robinson was carried out at approximately the same time to investigate the regional variations in the seasonality of the copepod *Calanus* (Matthews, 1969). Matthews revealed differences in seasonality between *C. finmarchicus*, *C. helgolandicus*, and *C. glacialis*, and important regional differences in the seasonality of *C. finmarchicus*. These results have been confirmed and extended in recent studies (Planque *et al.*, 1997; Planque and Batten, 2000). Timing in seasonality of *C. finmarchicus* can vary by up to four months (Figure 3), reflecting profound variations in the life-cycle strategy and population dynamics of the species in different areas of the North Atlantic.

The study of seasonality has extended to almost every taxonomic group sampled by the survey: fish larvae (Bainbridge *et al.*, 1974; Coombs, 1980; Coombs and

Mitchell, 1981), thaliacea (Hunt, 1968), decapod larvae (Lindley, 1987; Lindley *et al.*, 1993), pteropods (Cooper and Forsyth, 1963), gastropods (Vane and Colebrook, 1962), and countless contributions on phytoplankton and copepods (see the compilation of bibliography in the *CPR Atlas of Oceanographic Laboratory of Edinburgh*, 1973 and at the SAHFOS Website: www.npm.ac.uk/sahfos/).

Long-term changes

Studies of the long-term variations in plankton populations require long data series. This may read as a trivial statement, but the acquisition of the long-term data sets needed for these studies certainly is not. The CPR survey has succeeded in that effort and, as the series has been lengthening, empirical evidence on the long-term variability in plankton has been gathered to an extent that has no equivalent elsewhere.

The first report on long-term fluctuations derived from the CPR was concerned with fish eggs and larvae in the North Sea and was published 22 years after the start of the survey (Henderson, 1953). This comparative study of pre- and post-war years (14 years of data in total) revealed the large amplitude of year-to-year changes in young fish abundance together with the association between the recorded density of eggs and the size of the spawning stocks reflected in the fisheries captures. The next account was published four years later and presented results on the populations of *Calanus helgolandicus* and *C. finmarchicus* in the North Sea (Rees, 1957). However, in this contribution, little was discussed of the long-term changes in populations, and the eight years of data presented were treated as replicates. It is in the following paper of the same volume that Rae (1957) provided the first true description of long-term changes in plankton populations with a study of the copepod *Metridia lucens* over 10 years. Long-term studies soon addressed the question of changes in the composition of the plankton community as first presented in the study by Glover (1957) followed by that of Williamson (1961), both using results from the plankton indicator.

One of the most significant contributions in this area is the work developed by Colebrook on the principal component analysis (PCA) of phytoplankton and zooplankton (PCA is equivalent to the analysis of EOFs – empirical orthogonal functions – commonly used in meteorology, keeping with Hardy's visionary idea of analysing plankton data in the same way as meteorological ones). The results of the PCA showed 1) that variability in plankton occurs at all time scales, and that long-term trends can often account for the largest fraction of the variance, 2) that many species share common traits in their phenology, and 3) that the interannual variability in plankton is spatially structured, and in particular that changes in abundance of species off the

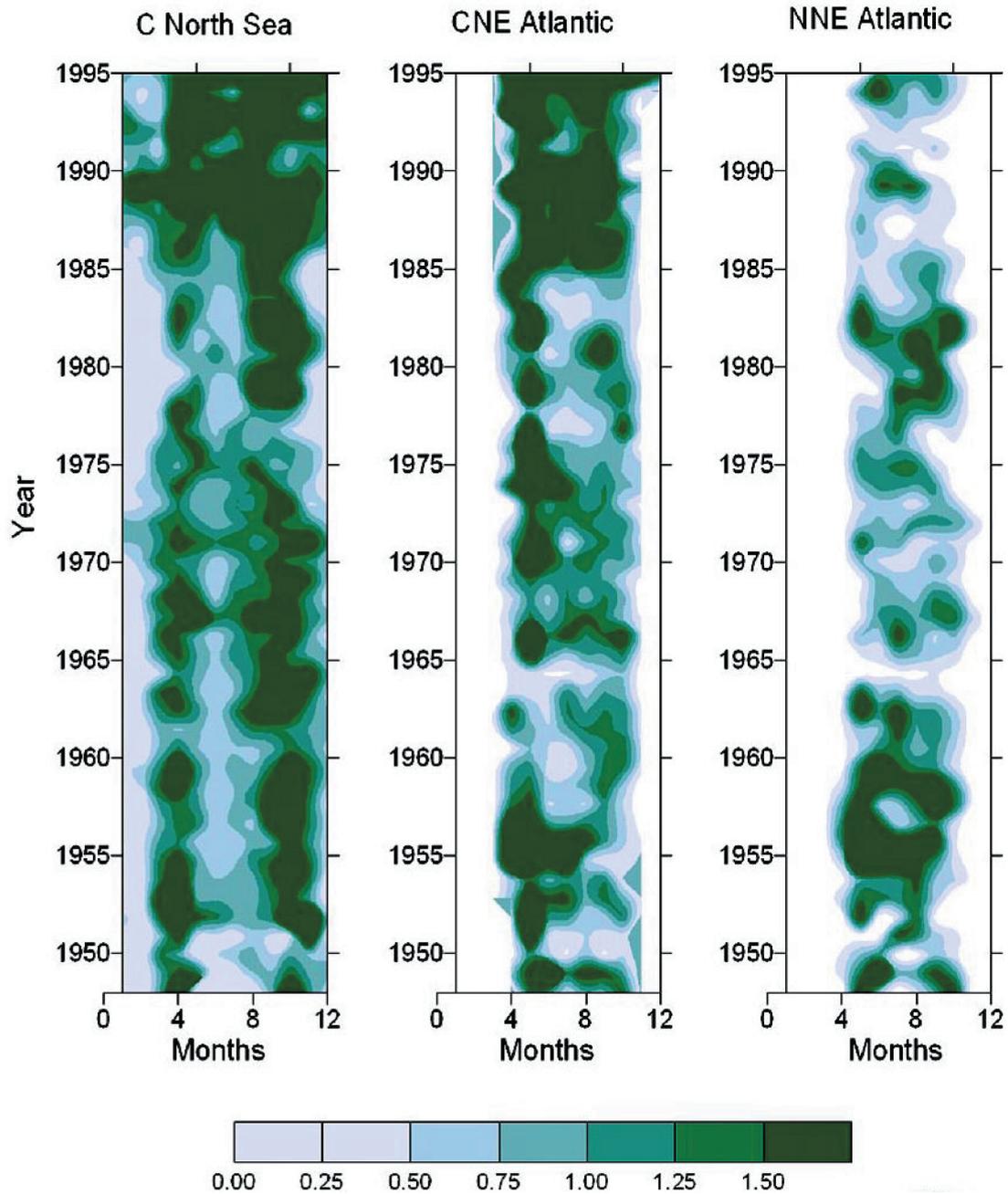


Figure 2. Contour plots of mean monthly phytoplankton colour during 1948–1995 for the central North Sea, the central Northeast Atlantic, and the northern Northeast Atlantic (redrawn from Reid *et al.*, 1998).

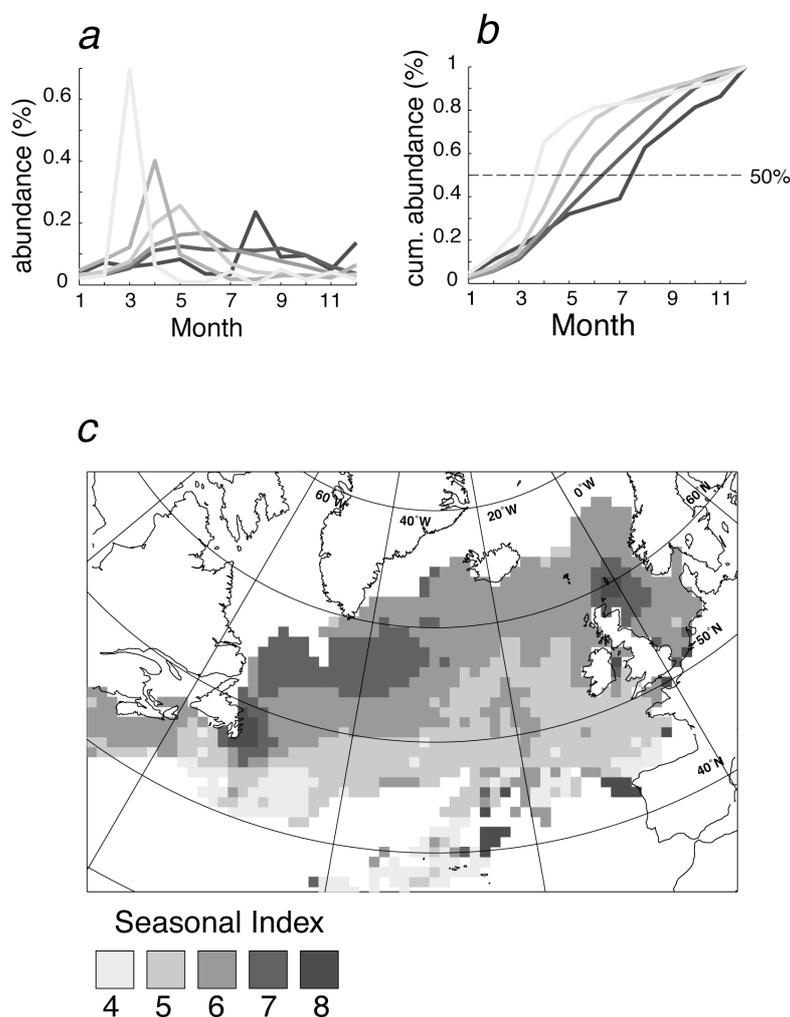


Figure 3. Spatial variations in the seasonal abundance of *C. finmarchicus*. Grey intensity is proportional to local value of the seasonal index. The seasonal index is the month at which 50% of the total annual abundance of *C. finmarchicus* has been collected by the CPR survey. Increasing seasonal indices correspond to later seasonality in the abundance of *C. finmarchicus*. Spatial variations in the seasonal abundance of *C. finmarchicus*. (a) Mean time-series of monthly abundance, (b) cumulated time-series of monthly abundance, and (c) spatial distribution of the seasonal index showing geographical variability in seasonality (redrawn from Planque and Batten, 2000).

European shelf are distinct from those occurring in-shelf (Colebrook, 1969; Colebrook, 1978; Colebrook *et al.*, 1984; Colebrook and Taylor, 1984; Colebrook, 1985). The importance of these results is probably best summarized in the representation of the first principal components of phytoplankton and zooplankton in the Northeast Atlantic (Figure 4a, b) in which it is clear that changes in abundance at the longest time scales take up most of the interannual variability. It has recently been estimated that the decline in copepod abundance recorded by the survey led to a decrease in the biomass of this group by approximately 50% in the Northeast Atlantic

(Figure 4c) (Planque and Batten, 2000). It is not yet clear whether such a reduction in copepod biomass has been balanced by an increase in the biomass of other taxonomic groups or if it reflects a general decline in the standing stock of zooplankton in this region.

Links with hydroclimatic changes

The link between plankton and its environment was recognized from the beginning by Hardy, but it was only in 1946 that an article dedicated to the study of plank-

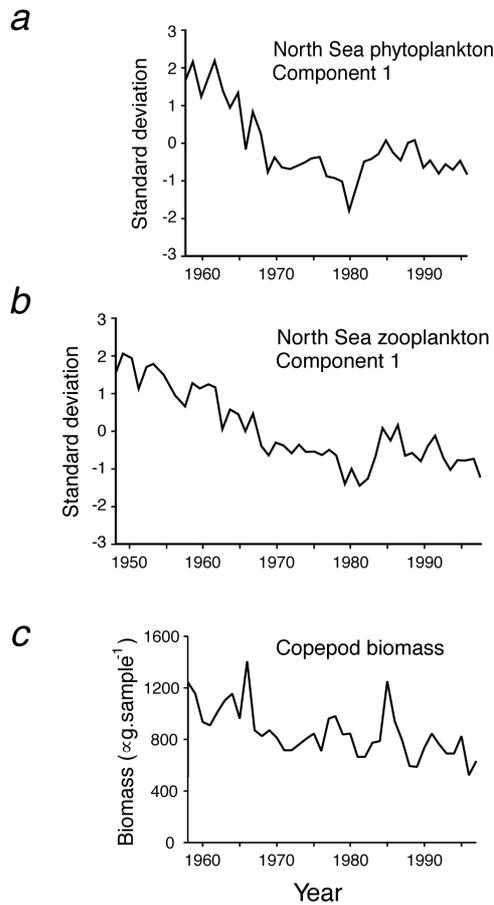


Figure 4. Changes in the abundance of plankton in the Northeast Atlantic: First Principal Components of (a) phytoplankton and (b) zooplankton in the North Sea (for details of the method see Colebrook, 1978), and (c) changes in the total biomass of copepods around the British Isles (redrawn from Planque and Batten, 2000).

ton in relation to hydrography was published by Lucas and Rae (1946). Unfortunately, the report by Lucas and Rae was only the first part of this research and dealt exclusively with hydrography. The second part, which discussed the relation of hydrography to plankton, was never published as such. Although, two decades later, large amounts of work still concentrated on the relationship between plankton distribution and the distribution of water masses (see e.g., Bary, 1963). The study of plankton phenology in relation to changes in the environment only started when the survey reached its multi-annual status. The first work on long-term changes in plankton derived from the CPR addressed the three objectives of Hardy's "Explanation": 1) the description of long-term changes in plankton, 2) their relation to

environment, and 3) their impact on fisheries (Rae, 1957). In this contribution, Rae presented empirical evidence for the effects of wind on the transport of the copepod *Metridia* into the North Sea and its connection to year-class strength in haddock populations. CPR records have been used subsequently many times to study the linkages between changes in the North Atlantic water inflow and plankton distribution and abundance in the North Sea (e.g., Glover, 1957; Bainbridge and Forsyth, 1972; Lindley *et al.*, 1990; Reid *et al.*, 1992; Stephens *et al.*, 1998; Corten, 1999; Edwards *et al.*, 1999; Heath *et al.*, 1999).

The changes in winds during the last decades not only affected circulation patterns, but also the vertical mixing of the water column with consequences on the development of stratification and the level of turbulence encountered at the scale of planktonic organisms. Wind-related changes in stratification have been extensively studied, and their impact on primary production has been clearly presented by Dickson *et al.* (1988). On a large spatial scale, the changes in the general distribution of the wind field in the North Atlantic and their relationship to the frequency of westerly weather over western Europe has been related to changes in the general trends of phyto- and zooplankton in a number of contributions (e.g., Aebischer *et al.*, 1990; Colebrook, 1991).

Another well-known environmental relationship derived from the CPR is the link between the latitude of the north wall of the Gulf Stream in the western North Atlantic and the abundance of total copepods recorded by the survey in the Northeast Atlantic. The relationship that was first proposed by Taylor and Stephens (1980) still holds two decades later (Taylor, 1995), but at the same time, the underlying mechanism is still unknown despite the many hypotheses that have been proposed to account for this relationship. The Gulf Stream index (GSI) is most certainly a proxy for large-scale changes in the ocean-climate system of the North Atlantic, and it was suggested by Taylor and Stephens (1998) that shifts in the Gulf Stream could be attributed to atmospheric changes reflected in the North Atlantic Oscillation (NAO) two years previously. This is now questioned by Joyce *et al.* (2000) who have determined an alternative index for the latitude of the Gulf Stream which varies in synchrony with the NAO rather than with a lag of two years.

More recently, the possible effects of the North Atlantic Oscillation (NAO) on the plankton of the Northeast Atlantic have been suggested by Fromentin and Planque (1996). In their study, they showed that the abundance of two dominant copepod species, *Calanus finmarchicus* and *C. helgolandicus*, was strongly related to the state of the NAO. The increase in the NAO index during the past four decades has been paralleled with a decrease in the abundance of *C. finmarchicus* by nearly 80% (Planque and Batten, 2000). To explain this relationship, several hypotheses have been put forward (Fromentin and Planque, 1996; Planque and Taylor,

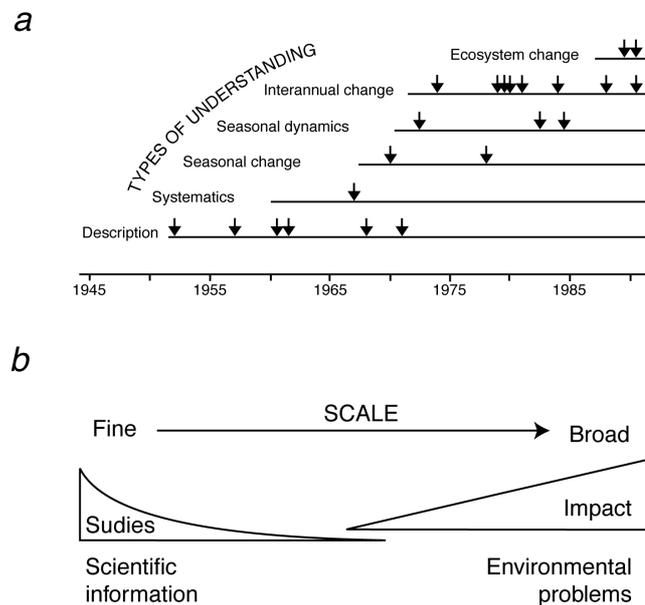


Figure 5. (a) The progressive elaboration of our understanding as the CPR time-series lengthens, illustrated by the date and type of key papers from the postwar bibliography of the CPR survey (redrawn from The Case For GOOS 1992, in Dickson, 1995). (b) Scale differences between environmental management problems and the answer that may be found in ecological studies (redrawn from S. F. Thrush in Legendre and Legendre, 1998).

1998; Stephens *et al.*, 1998; Heath *et al.*, 1999). However, the recent breakdown in the *Calanus*-NAO relationship since 1996 suggests that the significance of the NAO index as a proxy for environmental changes in the North Sea might have changed or that shifts in the plankton system of the North Sea could have overridden the effects of the NAO and contributed to the decline of *C. finmarchicus*, despite a return to an extreme low NAO situation in early 1996.

Changes in the planktonic ecosystem, trends and shifts

Apart from the detection of changes in single-species abundance, the CPR survey, with nearly 400 taxa identified, has been a tool of choice for the detection of changes in the plankton community. The principal component analysis of phyto- and zooplankton revealed trends that were common to most species of these two groups (Figure 4a, b). The analysis by Colebrook (1978) revealed the high degree of coherence between the taxa sampled by the survey, supporting the hypothesis of density-independent climate control of the Northeast Atlantic plankton. These changes in abundance have

also been associated with changes in the seasonal timing of plankton production (Reid, 1975; Radach, 1984). The cascading effects of climate variability on several trophic levels was presented in a study by Aebischer *et al.* (1990), who reported a marked parallelism between times-series of climate, plankton, fish, and marine bird species around the UK.

Recently, dramatic changes in the plankton and fish community of the North Sea associated with critical changes in the hydroclimatic environment have been reported by Reid *et al.* (2001). After 1987, the colour index recorded by the survey sharply increased both in intensity and seasonal extent (Figure 2), while at the same time, marked changes in phytoplankton and zooplankton species were observed. These changes coincided with an increased flow of North Atlantic water into the North Sea, which is likely responsible for the observed large increase in the catches of horse mackerel (*Trachurus trachurus*) in the northern North Sea.

Conclusion

Over 70 years of sampling, the results from the CPR survey have provided a unique source of information for

our understanding of the planktonic ecosystem in the North Atlantic and its connection with climate and fisheries variability in this region. From geographical description of single species to regime shifts, the survey has demonstrated the versatility of large-scale, long-term studies. The nature of the results derived from the survey has evolved as the survey has become older, from species description and geographical description of single species to shifts in the planktonic ecosystem (Figure 5a). The survey is now old enough to address some of the questions on environmental issues that are central to ICES, such as effects of climate variability and anthropogenic forcing on marine ecosystems (Figure 5b). An additional consequence of its lengthening is that the CPR time-series has become the reference for a number of other time series or short-term field investigations by setting up a multidecadal context with which to compare present results. This aspect has been the most valuable to ICES. It was important, directly, when ICES and OSPARCOM assumed joint responsibility for the North Sea Task Force and, using CPR records, were able to provide support for large-scale climatic forcing on phytoplankton against local anthropogenic causes (North Sea Task Force, 1993). It has been important, indirectly, in numerous ICES working groups which have used the CPR information as a reference for the interpretation of ICES series (for example, the ICES Cod and Climate Change Backward-Facing Working Group, or the Working Group on Zooplankton Ecology). ICES and CPR time-series have been used jointly in numerous works to study the relationships between changes in fish populations, their environment, and their food (e.g., Aebischer *et al.*, 1990; Reid *et al.*, 2000; Brander, 1992).

As shown by Steele (1985) in a comparative study of marine and terrestrial ecosystems, variability in marine populations is generally highest at large spatial-temporal scales because these are the scales at which the environmental variability is greater. As the CPR time-series has lengthened, it has become clearer that the greatest variations in plankton are indeed observed at the largest time-space scales, and the links between fish, plankton, and climate variability have become clearer and statistically more robust. Results from the CPR survey have emphasized the complex nature of planktonic systems in the North Atlantic and have revealed the existence of abrupt and unsuspected changes in unexploited systems. The CPR large-scale survey remains essential to detect the unpredictable.

ICES has played a major role in the initiation and maintenance of environmental and biological monitoring programmes in the North Atlantic. ICES is the home of time-series and has, throughout the 20th century, been the body charged with the maintenance and interpretation of what are now the "jewels of ICES". The CPR survey has shared the same dedication towards monitoring and, together with ICES, has worked to improve our understanding of the oceanic ecosystems over the scale of greatest variability: the multi-decadal scale.

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