

# Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow

PHILIP C. REID,<sup>1,\*</sup> MARTIN EDWARDS,<sup>1</sup>  
GREGORY BEAUGRAND,<sup>1</sup> MORTEN  
SKOGEN<sup>2</sup> AND DARREN STEVENS<sup>1</sup>

<sup>1</sup>Sir Alister Hardy Foundation for Ocean Science, The  
Laboratory, Citadel Hill, Plymouth, Devon PL1 2PB, UK

<sup>2</sup>Institute of Marine Research, PO Box 1870, Nordnes, Bergen,  
N-5817, Norway

## ABSTRACT

Oceanic inflow is estimated to contribute more than 90% of the nutrient input into the North Sea. Variability in the volume, chemical properties, biological content and source of the inflowing water is thus likely to have a considerable effect on North Sea ecosystems. Changes seen in the plankton, and in particular *Calanus finmarchicus* and *Calanus helgolandicus*, over the last 40 years as measured by the Continuous Plankton Recorder survey, allow clear periods to be identified that appear to be associated with variability in inflow. Monthly estimates of inflow and outflow across a section between Orkney and Utsira in Norway as well as netflow (sum of Baltic outflow, runoff and Channel inflow), have been derived from runs of the NORWECOM model for two integrated depth intervals: surface to 150 m and >150 m. A comparison is made between the physical model output and plankton results for the period 1958–99. Distinct plankton periods that appear to reflect changing inflow events are discussed in relation to hydrometeorological and earlier plankton studies over approximately the last 100 years.

**Key words:** atmospheric forcing, fisheries, hydrographic variability, inflow modelling, oceanic inflow, slope current, zooplankton

## INTRODUCTION

The volume and source of inflowing oceanic water to the North Sea, in terms of nutrient content, is likely to

have a major impact on ecosystem productivity as it is estimated that 90% of the annual input of nutrients is derived from this source (NSTF, 1993). Variability in these inflows is thus likely to affect the carrying capacity for fish resources and in turn the composition and tonnage of fish landings. Early evidence demonstrating variability in the source and volume of inflowing oceanic water was shown from indicator plankton (Fraser, 1969) and from salinity (Dickson, 1967, 1971), but until recently this aspect of North Sea ecosystem variability has been largely ignored as anthropogenic impacts from eutrophication, contamination and fisheries have been the main focus to explain ecosystem variability. Recent work from the Continuous Plankton Recorder (CPR) survey and three-dimensional physical (3D) modelling has helped to reinforce the importance of oceanic inflow as a driving force for changes in the North Sea (Reid and Edwards, 2001; Edwards *et al.*, 2002). In this paper, we present:

1. Changes in the abundance of two of the largest and most important copepods in the North Sea: *Calanus finmarchicus* and *Calanus helgolandicus* for the period 1958–2000 to demonstrate evidence for different 'biological periods' that may be related to inflow events;
2. A comparison between these findings and the results of the wind driven NORWECOM 3D model for measured inflow, outflow and netflow at two depth intervals, 0–150 and 150–500 m;
3. A retrospective analysis of evidence for other inflow events from 1900 to 1957 based on published information on biological, chemical and physical events.

## MATERIALS AND METHODS

### *Continuous Plankton Recorder*

A network of transects along which CPRs are towed monthly across the major geographical regions of the North Atlantic has been operated, with a break during the Second World War, since 1931. The CPR is a high-speed sampler (usually towed between 10 and 18 knots), sampling at a depth of approximately 10 m. After the tow, the CPR is returned to the laboratory for routine analysis involving the estimation of

\*Correspondence. e-mail: pcre@mail.pml.ac.uk

Received 11 November 2002

Revised version accepted 2 June 2003

phytoplankton biomass (phytoplankton colour index) and the quantification of zooplankton and phytoplankton taxa (Warner and Hays, 1994).

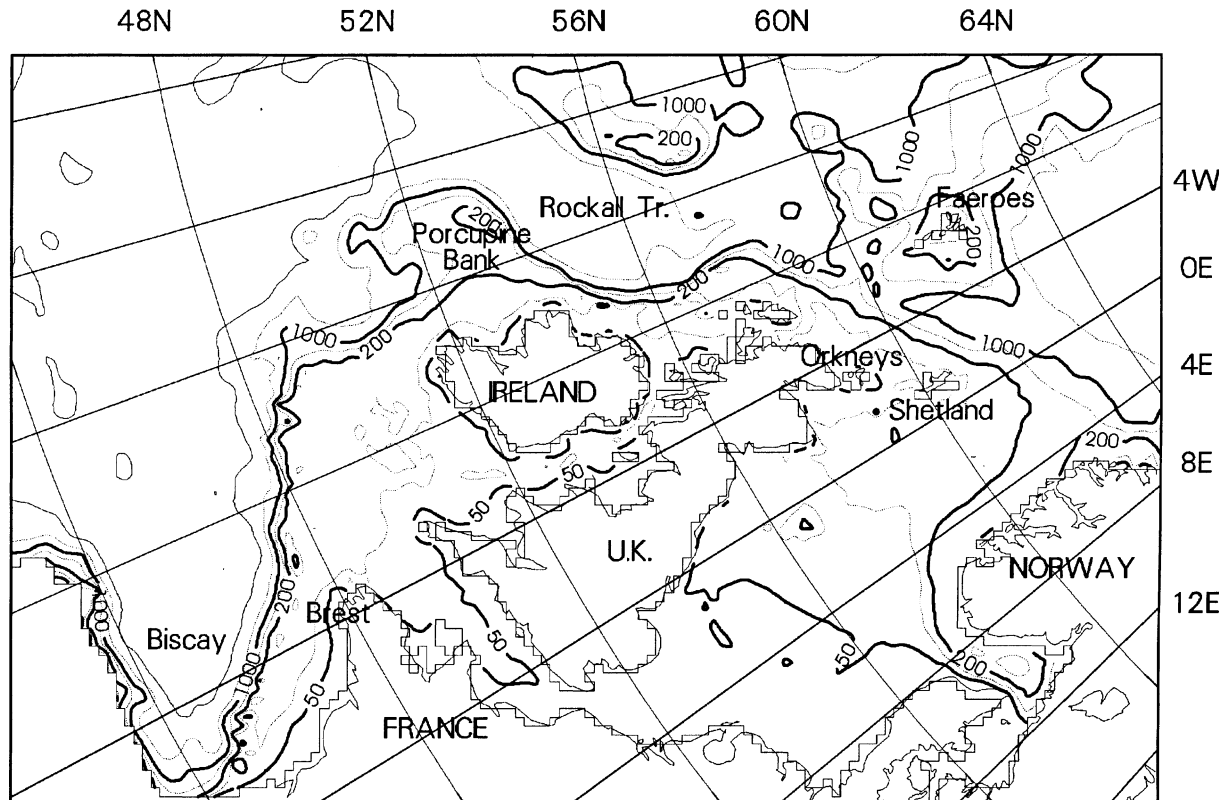
*The NORWEGIAN eCOlogical Model system (NORWECOM)*

A coupled physical, chemical and biological model system NORWECOM (Aksnes *et al.*, 1995; Skogen *et al.*, 1995; Skogen and Sjøiland, 1998) has been developed and used in studies of primary production, nutrient budgets and dispersion of particles such as fish larvae and pollution (e.g. Skogen and Moll, 2000). Validation of the model system has been achieved by comparison with field data in the North Sea and Skagerrak (Svendsen *et al.*, 1995, 1996; Berntsen *et al.*, 1996; Skogen *et al.*, 1997; Sjøiland and Skogen, 2000). The circulation module is based on the wind and density driven primitive equation Princeton Ocean Model (Blumberg and Mellor, 1980). A 20-km horizontal grid covering the whole shelf area from Portugal to Norway, including the North Sea, has been used (Fig. 1). The forcing variables are 6-hourly hindcast atmospheric pressure fields provided by the Norwegian Meteorological Institute (DNMI)

(Eide *et al.*, 1985; Reistad and Iden, 1998), 6-hourly wind stress (translated from the pressure fields by assuming neutral air-sea stability), four tidal constituents and freshwater runoff. Initial values for velocities, water level, salinity and temperature are taken from monthly climatologies (Martinsen *et al.*, 1992). Interpolation between these monthly fields is used along the open boundaries, except for the Baltic where the volume fluxes have been calculated using the algorithm of Stigebrandt (1980). To absorb inconsistencies between forced boundary conditions and model results, a seven-grid cell 'Flow Relaxation Scheme' zone is used around the open boundaries (Martinsen and Engdahl, 1987). Owing to a lack of data on surface heat fluxes, a 'relaxation towards climatology' method was used (Cox and Bryan, 1984). During calm wind conditions the surface temperature field adjusts to the climatological values after about 10 days (Oey and Chen, 1992). The net evaporation precipitation flux is set to zero.

Each simulation was started on 15 December, and after a 2-week spin-up time, model results were stored from 1 January to 31 December. The model was then re-initialized and run for the next year. Based on the

**Figure 1.** A map showing the region included in the NORWECOM model domain with a superimposed bathymetry.



modelled current fields, average monthly inflow, outflow and netflow (the sum of Baltic outflow, river runoff and fluxes through the Channel via the Dover Strait) through an east–west section from Utsira on the Norwegian west coast to the Orkney Islands (along 59°17' N) in the northern North Sea were computed for all years from 1958 to 1999 and averaged for two depth intervals, 0–150 and >150 m.

*Comprehensive Ocean-Atmosphere Data Set (COADS)* Monthly means of scalar wind, U and V winds (south to north and east to west components of wind, respectively) were averaged from COADS (Woodruff *et al.*, 1987) one-degree data for the area 55°N–60°N, 5°W–5°E over the period January 1958 to December 1999. The data were provided by the NOAA-CIRES Climate Diagnostics Center (Boulder, CO, USA).

#### North Atlantic Oscillation (NAO)

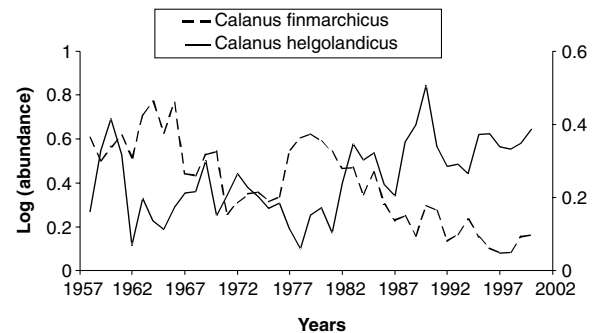
In the North Atlantic, the dominant mode of atmospheric pressure variability is the NAO. An index of the variability of the NAO is derived from the alternation of atmospheric mass between subtropical, high-surface pressures (centred over the Azores) and sub-polar, low surface pressures (centred over Iceland) and accounts for more than one-third of the total variance of sea level pressure in the North Atlantic (Dickson and Turrell, 2000). Decadal trends in this index influence regional temperatures and precipitation, and the degree of wind speed/direction over northern Europe (Hurrell, 1995).

## RESULTS

#### *Calanus* and inflow

The abundance of the boreal copepod *C. finmarchicus* and warm temperate congeneric *C. helgolandicus* has shown a systematic alternation in abundance in the North Sea over the last 40 years (Fig. 2). In part, this reflects the inverse correlations that the two species show with the NAO (Fromentin and Planque, 1996; Planque and Fromentin, 1996). Although the relationship between the NAO and *C. finmarchicus* has been broken down since 1996 (Planque and Reid, 1997), a strong relationship with sea surface temperature (SST) is also evident for *C. helgolandicus*, which in the North Sea can be considered as a biological thermometer (Lindley and Reid, 2002). When expressed as the ratio of *C. helgolandicus* to *C. finmarchicus* (Fig. 3), the regime shift identified by Reid *et al.* (2001a) is clearly distinguished. This event was shown to be strongly related to increased inflow of oceanic water from the

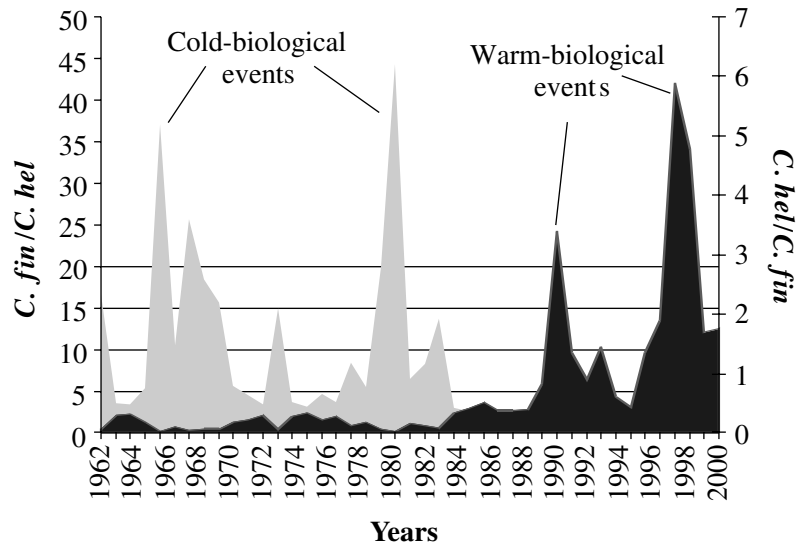
**Figure 2.** Graphs of the log abundance of *C. finmarchicus* (solid line) and *C. helgolandicus* (dashed line) averaged for the North Sea over the period 1958–2000.



Atlantic (Reid *et al.*, 2001a) with a southerly source and this also appears to be linked to higher flows in the slope current to the west of the British Isles (Holliday and Reid, 2001; Reid *et al.*, 2001b). The two peaks evident in the ratios also coincide with the two major incursions demonstrated by the intrusion of southerly plankton into the North Sea (Edwards *et al.*, 2001; Holliday and Reid, 2001).

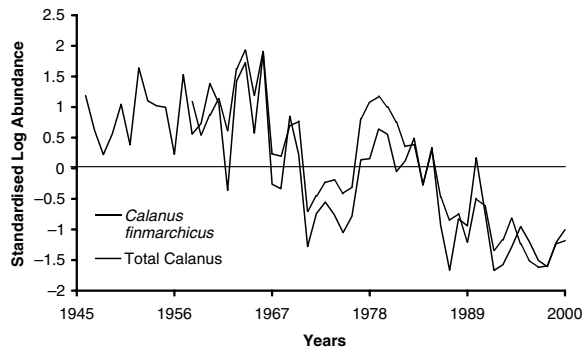
If expressed as the reverse ratio of *C. finmarchicus* to *C. helgolandicus* (Fig. 3), two other periods are identified: a 'cold' biological event between approximately 1978 and 1982, and an earlier 'cold' event between approximately 1962 and 1967. In the earlier period *C. finmarchicus* was abundant in the North Sea. The two species were not distinguished in CPR analysis prior to 1958, but because *C. finmarchicus* is on average 10 times more abundant than its 'sister' species, a comparison has been made between *C. finmarchicus* and total *Calanus* over the period 1958–2001 (Fig. 4); the relationship is very close ( $r = 0.85$ ;  $P = 0.01$ ). If this relationship holds for the period prior to 1958 and back to 1946 it suggests (Fig. 4) that *C. finmarchicus* also dominated the plankton of the North Sea over the period 1946–57.

If the relative abundance of these two copepod species is expressed in percentage terms (Fig. 5), a clear trend in their relative abundance is evident with a notable change in the trend in the years 1978–82 first identified in Reid *et al.* (2000). Then this 'cold biological event' was attributed to a 'top down' density driven modulation from the fishery. There may still be a density driven component during these years, but it would now appear that this change is physically forced (Reid and Edwards, 2001; Edwards *et al.*, 2002). The 1978–82 event is also distinguished in the plankton by the presence in the North Sea and especially in the Norwegian Trench, of a suite of plankton

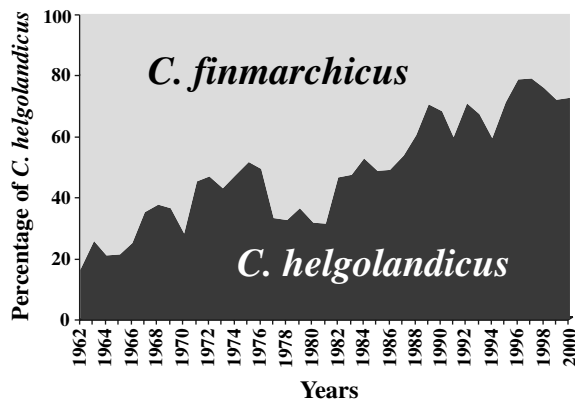


**Figure 3.** Plots of the relative ratios of *C. helgolandicus* to *C. finmarchicus* shaded in black and right axis and the reverse ratio, left axis and shaded in grey over the same period as in Fig. 1.

**Figure 4.** Standardized plots of the abundance of *C. finmarchicus* (solid line) with superimposed total *Calanus* (dashed line) averaged for the North Sea between 1946 and 2000.



**Figure 5.** A plot of the relative percentage abundance of *C. finmarchicus* and *C. helgolandicus* (1962–2000).



characteristic of boreal waters (e.g. *Calanus hyperboreus*, *Metridia longa*, *Navicula planemembranacea*; see Reid and Edwards, 2001), plus a wide range of other associated changes in plankton, fish and hydrographic properties (Edwards *et al.*, 2002).

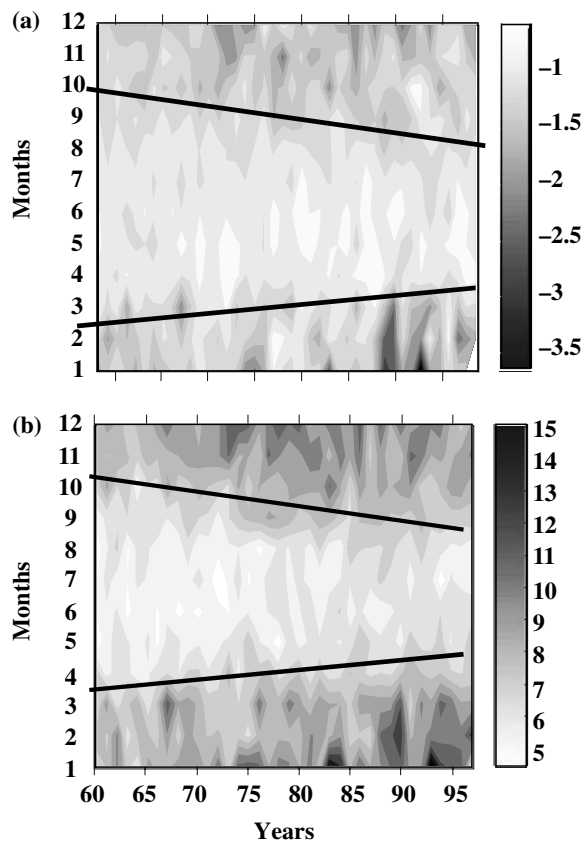
Characterization of the ~1962–67 period is less clear and has been less rigorously examined to date. It would appear to again represent a time of lower oceanic inflow with reduced penetration of 35 salinity (see Fig. 9 of Reid *et al.*, 1992) water into the North Sea.

*NORWECOM modelled inflow/outflow*

As the main Atlantic inflow to the northern North Sea is wind driven, the model is forced by realistic wind and pressure fields. In addition, the model is run in prognostic mode to include both the baroclinic and barotropic components of the transport. Other external forcings such as the strength of the slope current might also generate variability in the inflow, but this is only partially accounted for in the model used here (Fig. 1). Modelled inflow to the northern North Sea is shown in Fig. 6(a). A clear trend is evident over the period 1958–99 to a shortened period of lower inflow in the summer with an increasing intensity and longer period of strong inflows during the rest of the year. A similar plot for scalar winds (Fig. 6b) shows the same pattern demonstrating the clear linkage between wind and the model results.

Figure 7 shows the results for inflow and outflow in the same format as above for two depth intervals 0–150 and >150–500 m. From the perspective of the model, 500 m represents the bottom of the Norwegian Trench. Clearly evident in the inflow and outflow

**Figure 6.** (a) A contour plot of modelled oceanic inflow into the North Sea (surface to bottom) across a section between Orkney in Scotland and Utsira in Norway averaged for each month between 1958 and 1999 (Sverdrups). Left axis, months. (b) Scalar wind averaged for the area 55°N 60°N 5°W 5°E, plotted as for 'a' ( $\text{m s}^{-1}$ ). Lines have been delineated on the figures to emphasize the similarity in the seasonal changes seen in both parameters.



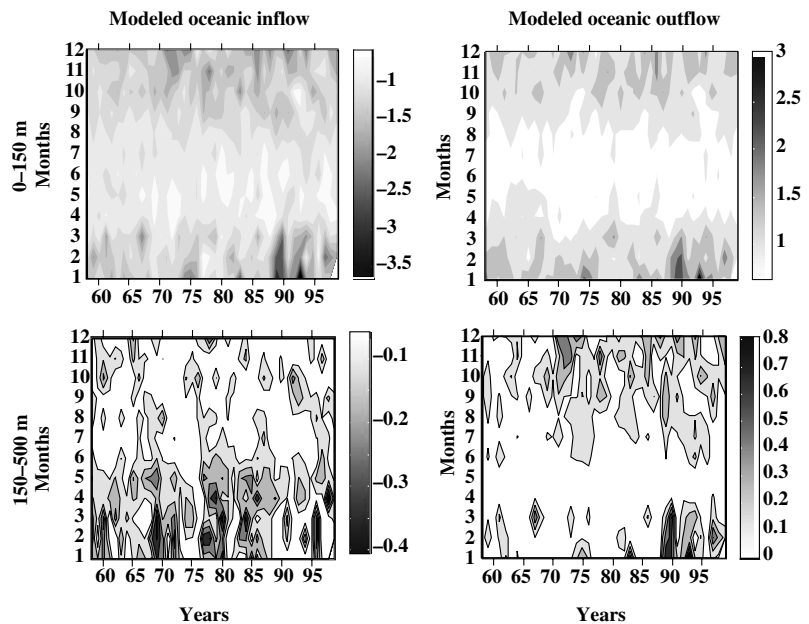
plots for the upper layer is the increased winter inflow post-1987 that corresponds with the regime shift identified by Reid *et al.* (2001a). (A regime shift is a large decadal scale switch in the abundance, productivity and composition of plankton, fish and other biota that is associated with hydroclimatic changes of a similar scale.) The circa 1988 regime shift in the North Sea is evident as a step-wise change in all trophic levels of the ecosystem as well as a range of physical variables, nutrients and oxygen (Reid and Edwards, 2001; Reid *et al.*, 2001a). Outflow in this upper layer was minimal in the stratified summer months of the year. Enhanced outflow also occurred in most years subsequent to 1987 in the upper 150 m with low inflow especially in the first 3 months of the year below 150 m. The 1978–82 event is most evident in the reduced netflow in the upper layer (Fig. 8) in

the early months of the year and higher inflow and net flow at the same time in the water layer below 150 m (Figs 7 and 8). Netflows (Fig. 8) in the upper layers appear to be generally lower in the first 6 months of the year and the reverse in the lower layer. The anomalously high inflow event of the autumn of 1972 is evident in Fig. 7, but especially so in netflows (Fig. 8). This event was characterized in the plankton by the incursion of the doliolid *Doliolletta gegenbaui*. There is little evidence from the modelled transports for anomalous variability in the period 1961–66 other than generally low inflow in the upper layer. A more detailed analysis of inflow anomalies in relation to the presence of planktonic indicators is the subject of ongoing research. The next section of this paper provides a preliminary synthesis of historical evidence from the twentieth century to place the modelling results presented here in a longer-term context.

The modelled data used in this study were originally derived from flow averaged over four depth intervals, 0–30, 30–50, 50–150 and 150–500 m. A Principal Component Analysis was carried out on all monthly flows over the period 1958–99 for all depth intervals. The resulting First Principal Component shows a positive relationship between inflow in the depths between 0 and 150 m and a negative relationship for waters below 150 m ( $r = 0.64$ ;  $P = >0.001$  after autocorrelation was taken into account). Variables that were related positively to this Principal Component were the inflow between 0 and 150 m in the first 3 months of the year (+NAO = high inflow); below 150 m the relationship was opposite (e.g. +NAO = low inflow). Given the known high correlation between the NAO and scalar winds in the first quarter of the year in the northern North Sea (Dickson and Turrell, 2000; Reid and Planque, 2000) this relationship is not surprising as the flows are a local response to large-scale atmospheric forcing. The correlation between inflow and the NAO (Fig. 9) re-emphasizes the important role that the pressure gradient reflected by the NAO plays in hydrometeorological variability in the North Sea.

#### *Historical evidence for inflow events in the twentieth century*

The CPR has systematically surveyed the North Sea on a monthly basis since 1946. Records from the survey suggest that particularly high numbers of oceanic plankton species were recorded in the early 1950s, 1972, in the late 1980s, early 1990s and in 1997/98 (Reid *et al.*, 1992; Edwards *et al.*, 1999). Using historical evidence from early plankton and fishery research cruises we have attempted to build a chronology of Atlantic inflow events that predates the



**Figure 7.** Contour plots as for Fig. 6 with inflow (on the left) and outflow (on the right) for the depths 0–150 m (upper panels) and 150–500 m (lower panels).

CPR survey back to the beginning of the twentieth century. The hydrobiological indicators include oceanic plankton (particularly thaliacea) and the presence of fish species in the North Sea that are normally characteristic of more southerly and shelf-edge habitats. Major swarms of thaliacea and southerly species recorded in the North Sea throughout the twentieth century are shown in Table 1. Physical data were also examined to determine the areal extent of Atlantic water (>35 PSU) and major salinity anomalies in the North Sea. Whilst many historical records have been examined, the major sources of information come from work previously published by Fraser (1961) and Dickson (1967). In Dickson's study, based on biological and physical evidence, he describes oceanic inflow events as 'Accelerated Atlantic inflow events'. Accelerated inflow events (pre-1950s) catalogued by Dickson (1967) include 1905–09, 1920–21, 1931–35, 1937–39 and 1949.

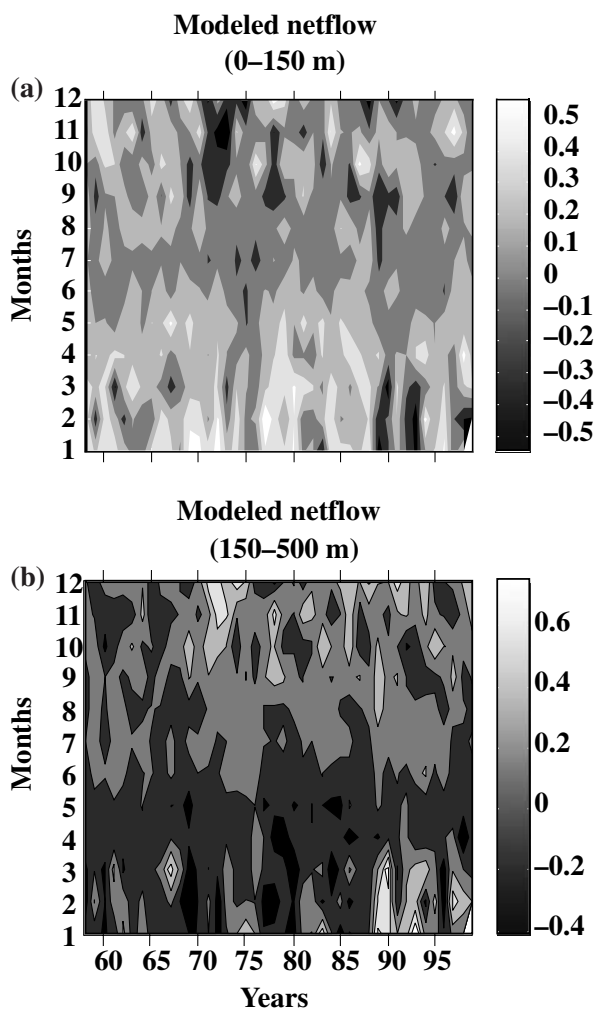
During the period 1900–25 particularly notable inflow events evidenced by high salinity anomalies were recorded between 1903 and 1906 and from 1920 to 1923 (Lucas, 1946). Deep water specimens of the fish genus *Arnoglossus* were recorded in the northern North Sea during 1904–06 suggesting a major inflow event (Dickson, 1967). In 1904–05, the Arctic-boreal euphausiid *Thysanoessa inermis* was common in the Norwegian Trench and Skaggerak. Other cold water species such as *C. hyperboreus* and *M. longa* were present throughout the North Sea between 1902 and 1906, at times even at the surface (Kramp, 1913). The Arctic species *C. hyperboreus* was also common in the

bottom waters of the Faroe-Shetland Channel and was found as far south as 54°N 30'W in the North Atlantic at this time. Huge drifts of 'distinctly' Atlantic salps (especially *Salpa fusiformis*) into the northern North Sea occurred in 1905 and 'enormous shoals' of the warm water pteropod *Spiratella lesueri* (not recorded north of the Bay of Biscay before 1906) were reported entering the English Channel in 1906 (Fraser, 1961).

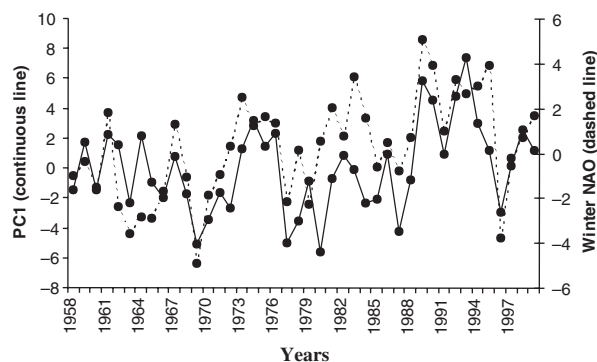
Dickson (1967) suggests that a minor accelerated inflow event occurred between 1912 and 1914. The only notable oceanic species recorded during this period was *Doliolum nationalis*, which was found in the Southern Bight in 1911 (Lindley *et al.*, 1990). The next major oceanic faunal invasion occurred between 1920 and 1923 when enormous swarms of *S. fusiformis* were noted in the northern North Sea (Fraser, 1949). Large numbers of pteropods and radiolarians were also noted in the North Sea during this period (Hardy, 1923).

The only inflow event that stands out between 1926 and 1950 as exceptional was during 1931–35. This period was marked by the presence of Mediterranean water in the Faroe-Shetland Channel and exceedingly high salinities in the Southern Bight in the autumn of 1933 (Dickson, 1967). Dickson also identified hydrobiological evidence for a major inflow event based on the incursion into the Baltic from the North Sea of horse mackerel (1932) and anchovy (1933) as well as noting a dramatic rise in the anchovy stock of the southern North Sea during the period 1930–34 and the occurrence of unusual warm-water fish species. Lucas (1933) noted the presence of Atlantic thaliacea (*D. gegenbauri*) in the northern

**Figure 8.** Contoured time series of modelled monthly mean netflows for surface (0–150 m) and bottom (150–500 m).



**Figure 9.** Graphs of the winter NAO (dashed line) with superimposed (continuous line) First Principal Component of a PCA analysis of water fluxes across the Orkney Utsira section for the depths 0–30, 30–50, 50–150 and 150–500 m (1958–2000).



North Sea in 1933. Other evidence for unusual hydro-climatic conditions around this period included major phytoplankton blooms in 1933 and 1934 of *Rhizolenia styliformis* and *Biddulphia sinensis* covering 7400 squares miles in the southern North Sea and the presence of *Sagitta elegans* in the Thames Estuary in 1933–34 (Dickson, 1967). In summary, three major Atlantic faunal invasions and salinity anomalies occurred in the North Sea in the first half of the twentieth century during 1903–06, 1920–22 and 1931–35.

**DISCUSSION**

From evidence collected by the CPR and other data sources it would appear that the plankton of the North Sea over most of the last century had a cold temperate character. The copepod *C. finmarchicus* is believed to have dominated copepod assemblages at least back to 1946 and from earlier CPR records would also appear to have been the dominant species in the 1930s. Information from other surveys indicates that colder conditions prevailed from the beginning of the twentieth century.

On the above pattern are superimposed two short periods when the North Sea had a more boreal character with incursion of species usually found much further to the north. The most recent of these events occurred between approximately 1978 and 1982 and had a profound effect on North Sea productivity, apparently even leading to a reduction in the total biomass of North Sea fish stocks (Reid and Edwards, 2001; Edwards *et al.*, 2002). The earlier period occurred during approximately 1902–06; at this time boreal species (e.g. *C. hyperboreus*, *M. longa*) were extensively distributed and common in the North Sea and even extended well south in the North Atlantic to the west (Kramp, 1913).

Two short warm events occurred during 1920–23 and 1931–35, in the latter there was evidence of a major incursion of horse mackerel into the North Sea, even extending into the Baltic, as well as extensive blooms of phytoplankton. These events show some of the characteristics (e.g. extensive phytoplankton blooms) of the period, with warm temperate zooplankton, which has prevailed until present following the regime shift that occurred around 1988. However, a preliminary examination of evidence from the CPR survey in the 1930s suggests that the plankton of the North Sea at that time had a cold temperate character. There is insufficient information available to determine if regime shifts have occurred at other times in the past. In terms of observed effects and its length, the present warm phase would appear to be

**Table 1.** Thaliacea in the North Sea from historical records between 1900 and 2000.

Records of Thaliacea in the North Sea	Year	Region
<i>Salpa fusiformis</i> (dense swarms)♀	1905	Northern North Sea
<i>Doliolum nationalis</i> ♀	1911	Southern Bight
<i>Salpa fusiformis</i> (dense swarms)♀	1920–22	Northern North Sea 55°N
<i>Salpa fusiformis</i> (dense swarms)♀	1925	Northern North Sea 55°N
<i>Dolioletta gegenbauri</i> ♀	1928	Northern North Sea 55°N
<i>Dolioletta gegenbauri</i> ♀	1933	Northern North Sea 57°N
<i>Salpa fusiformis</i> (dense swarms)♀	1954–55	Northern North Sea
<i>Dolioletta gegenbauri</i>	1972	Northern North Sea 56°N
<i>Doliolum nationalis</i>	1989	German Bight
<i>Doliolum nationalis</i>	1997	German Bight, Skagerrak

♀ Noted as reproducing in North Sea. According to Fraser (1949), the presence of reproducing populations indicates large influxes of warm oceanic water into the North Sea.

unique in at least the last century. The regime shift has had a pronounced impact on North Sea ecosystems evident in a range of altered hydrodynamic characteristics, step-wise changes in nutrient ratios and pronounced changes in both the abundance and composition of the plankton, benthos and other higher trophic levels. The growing season of the plankton (Edwards *et al.*, 2001) appears to have extended considerably and much of the phytoplankton appears to be ungrazed and settling to the bottom. Together these ecosystem changes are unfavourable to cold water demersal fish species such as the cod, are reinforcing the observed pronounced decline in their stocks and are complicating fishery management decisions that at present are based on models that do not take into account ecosystem variability.

The cold and warm biological events appear to be linked to increased (warm) and decreased (cold) inflows of oceanic water from the North Atlantic. In the case of the cold events the source of the colder water that is carrying the boreal indicator plankton derives from the Norwegian Sea via a deep inflow into the Norwegian Trench with the species subsequently undergoing vertical migrations and advection onto the shelf. The warm event after 1988 is consistent with modelled oceanic inflow and with higher oceanic inflows from the Slope Current that bring in water to the North Sea of a Lusitanian origin. (Lusitanian water masses are transported to the north at depth in the Rockall Trough, at times rising to the surface and have a southerly and possibly Mediterranean origin.) The enhanced inflows are generated by both increased wind strength and a change in the pattern of wind distribution with an increase in westerlies. These events are shown in turn to be highly correlated with the NAO and reflect regional changes in the climate of northwest Europe. The periodic strong inflows from

the Slope Current accentuate the overall changes, but the timing of their occurrence as occasional events on the basis of SST signals (Reid *et al.*, 2001b) does not appear to be directly linked to westerly winds or the NAO although time series data from current meters to check such a link are not available. Such inflows as occurred in 1988/89 and 1998 were followed by enhanced levels of phytoplankton biomass as measured by the CPR colour index. We expect that any future incursion of Lusitanian water into the North Sea will lead to a further enhancement in productivity and peak in the index of phytoplankton colour by analogy with the large increases in colour that coincided with the two previous examples.

Fromentin and Planque (1996) showed that the abundance of *C. finmarchicus* was highly significantly, inversely, related to the NAO, a relationship that broke down in 1996 (Planque and Reid, 1998). This species overwinters in a diapause state in deep water of the Norwegian Sea (and possibly at times the Norwegian Trench) and is most likely introduced to the North Sea via this route (Heath *et al.*, 1999) in deep inflow events, especially in the first quarter of the year. Examination of Fig. 7 shows that inflow of water below 150 m in the first quarter failed in years after 1987, fitting exactly the observed decline in the abundance of this species in the North Sea. In these years there was also, in contrast to the normal pattern, a strong outflow in the first quarter of the year; a time when any vertically migrating copepods from depth would be likely transported out of the North Sea along the Norwegian coast.

A major incursion of oceanic water below 150 m recurred in the spring of 1996 and should have led to a renewed influx of *C. finmarchicus* (Planque and Reid, 1998). But the expected recruitment did not happen, almost certainly because of a major reduction of the



overwintering stocks in the deep water of the Norwegian Sea (Heath *et al.*, 1999; Planque and Batten, 2000). Deep Norwegian Sea water, the overwintering habitat of these species, has been reducing in volume progressively because of a reduction in the formation of dense deep water in the Greenland Sea (Dickson *et al.*, 1996). The precise water mass conditions needed for overwintering are not known, but the volume available and possibly also its composition now appears to be unfavourable to overwintering. Further factors that are likely to have contributed to the disappearance of this species in the North Sea are the considerable northward biogeographic shift of cold boreal species like *C. finmarchicus* that has occurred over the last 40 years, the unfavourable warm temperatures for boreal species that have recently characterized the North Sea because of forcing by both the NAO and Northern Hemisphere temperatures (Beaugrand *et al.*, 2002) and a strong and warm Slope Current possibly preventing incursion of *Calanus* in the spring onto the shelf (Reid *et al.*, 2001b). Higher SSTs in the North Sea are correlated with a marked rise in Northern Hemisphere temperatures seen since the mid-1980s (Beaugrand *et al.*, 2002) and also with a positive NAO index as again seen predominantly since the mid-1980s (Reid and Planque, 2000).

This preliminary comparison of plankton time series measurements from the CPR and modelled fluxes of water into and out of the North Sea has revealed, at times, a close relationship between the plankton and hydrography. There is a suggestion that the ecology of *C. finmarchicus* is related to the pattern of deeper water inflow/outflow in the first half of the year shown by the model. Further work, including statistical analyses, are needed to test this suggestion. A conclusion that can be made from the evidence for the occurrence of periodic warm/cold events is that they are key forcing variables on North Sea ecosystems and similar events are likely to occur in other shelf seas. The patterns of change observed must have importance in developing an understanding of variations in the fish stocks of the North Sea. Furthermore, an integration of monitored plankton data and modelled hydrographic information may be of value in developing environmental input to new approaches to the management of fisheries. The model results need to be further validated by field measurements and the processes behind these previously undocumented variations in the patterns of vertically differentiated inflow and outflow examined. This study serves to reinforce the need to maintain long-term monitoring programmes of the plankton and the value of the standardized procedures applied over a long period of time by the CPR survey.

## ACKNOWLEDGEMENTS

The CPR survey would not be possible without the co-operation of the agents, owners, masters and crews of the vessels that tow the recorders. The survey is supported by a consortium comprising: IOC, UNIDO, the European Commission and agencies from Canada, Denmark, France, Faroes, Iceland, Ireland, the Netherlands, Portugal, the United Kingdom and the USA.

## REFERENCES

- Aksnes, D., Ulvestad, K., Balino, B., Egge, J. and Svendsen, E. (1995) Ecological modelling in coastal waters: towards predictive physical-chemical-biological simulation models. *Ophelia* **41**:5–36.
- Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A. and Edwards, M. (2002) Reorganisation of North Atlantic marine copepod biodiversity and climate. *Science* **296**:1692–1694.
- Berntsen, J., Svendsen, J. and Ostrowski, M. (1996) Validation and sensitivity study of a sigma-coordinate ocean model using the SKAGEX dataset. ICES C.M.1996/C:5.
- Blumberg, A.F. and Mellor, G.L. (1980) A coastal ocean model. In: *Mathematical Modelling of Estuarine Physics*. J. Sudman and K.P. Holtz (eds) Berlin: Springer Verlag, pp. 203–214.
- Cox, M.D. and Bryan, K. (1984) A numerical model of the ventilated thermocline. *J. Phys. Oceanogr.* **14**:674–687.
- Dickson, R.R. (1967) *Long-term changes in the hydrography of the European shelf seas since 1905, and the effects of these upon the distribution and abundance of various marine organisms*. PhD thesis, Univ. East Anglia. 164 pp.
- Dickson, R.R. (1971) A recurrent and persistent pressure anomaly pattern as the principal cause of intermediate-scale hydrographic variation in the European shelf areas. *Dt. Hydrogr. Z.* **24**:97–119.
- Dickson, R.R. and Turrell, W.R. (2000) The NAO: the dominant atmospheric process affecting oceanic variability in home, middle and distant waters of European Salmon. In: *The Ocean Life of Atlantic Salmon: Environmental and Biological Factors Influencing Survival*. D. Mills (ed.) Oxford: Fishing News Books, pp. 92–115.
- Dickson, R.R., Lazier, J., Meincke, J., Rhines, P. and Swift, J. (1996) Long-term coordinated changes in the convective activity of the North Atlantic. *Prog. Oceanogr.* **38**:241–295.
- Edwards, M., John, A.W.G., Hunt, H.G. and Lindley, J.A. (1999) Exceptional influx of oceanic species into the North Sea in late 1997. *J. Mar. Biol. Assoc. UK* **79**:737–739.
- Edwards, M., Reid, P.C. and Planque, B. (2001) Long-term and regional variability of phytoplankton biomass in the north-east Atlantic (1960–1995). *ICES J. Mar. Sci.* **58**:39–49.
- Edwards, M., Beaugrand, G., Reid, P.C., Rowden, A.A. and Jones, M.B. (2002) Ocean climate anomalies and the ecology of the North Sea. *Mar. Ecol. Prog. Ser.* **239**:1–10.
- Eide, L.I., Reistad, M. and Guddal, J. (1985) Database av berregnede vind og bølgeparametre for Nordsjøen, Norskehavet og Barentshavet: The Norwegian Meteorological Institute, Oslo, Norway. Report, 38 pp.
- Fraser, J.H. (1949) The distribution of Thaliacea in Scottish waters 1920–1939. *Fish. Invest.* **1**:1–44.

- Fraser, J.H. (1961) The oceanic and bathypelagic plankton of the north-east Atlantic and its possible significance to fisheries. *Mar. Res.* **4**:1–48.
- Fraser, J.H. (1969) Variability in the oceanic content of plankton in the Scottish area. *Prog. Oceanogr.* **5**:145–159.
- Fromentin, J.-M. and Planque, B. (1996) *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.* **134**:111–118.
- Hardy, A.C. (1923) Notes on the Atlantic plankton taken off the east coast of England in 1921 and 1922. *Publ. Circ. Cons. Perm. Int. Explor. Mer* **78**:5–10.
- Heath, M.R., Backhaus, J.O., Richardson, K. *et al.* (1999) Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. *Fish. Oceanogr.*, **8**:163–176.
- Holliday, N.P. and Reid, P.C. (2001) Is there a connection between high transport of water through the Rockall Trough and ecological changes in the North Sea? *ICES J. Mar. Sci.* **58**:270–274.
- Hurrell, J.W. (1995) Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science* **269**:676–679.
- Kramp, P.L. (1913) Resume plankton 1910–13: Schizopoda. *Conseil International pour l'Exploration de la Mer* **III**:539–556.
- Lindley, J.A. and Reid, P.C. (2002) Variations in the abundance of *Centropages typicus* and *Calanus helgolandicus* in the North Sea: deviations from close relationships with temperature. *Mar. Biol.* **141**:153–165.
- Lindley, J.A., Roskell, J., Warner, A.J. *et al.* (1990) Doliolids in the German Bight in 1989: evidence for exceptional inflow into the North Sea. *J. Mar. Biol. Assoc. UK* **70**:679–682.
- Lucas, C.E. (1933) Occurrence of *Doliolletta gegenbauri* (Uljanin) in the North Sea. *Nature* **132**:858.
- Lucas, C.E. (1946) The plankton of the North Sea in relation to the environment. *Hull Bull. Mar. Ecol.* **17**:1–33.
- Martinsen, E.A. and Engedahl, H. (1987) Implementation and testing of a lateral boundary scheme as an open boundary condition in a barotropic ocean model. *Coastal Eng.* **11**:603–627.
- Martinsen, E.A., Engedahl, H., Ottersen, G., Ådlandsvik, B., Loeng, H. and Balino, B. (1992) MetOcean Modelling Project. Climatological and hydrographical data for hindcast of ocean currents: The Norwegian Meteorological Institute, Oslo. Technical Report No. 100, 93 pp.
- North Sea Task Force (NSTF) (1993) *North Sea Quality Status Report 1993*. London: Oslo and Paris Commissions & Frederborg: Olsen & Olsen, 132 pp.
- Oey, L.Y. and Chen, P. (1992) A model simulation of circulation in the north-east Atlantic shelves and seas. *J. Geophys. Res.* **97**:20087–20115.
- Planque, B. and Batten, S.D. (2000) *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. *ICES J. Mar. Sci.* **57**:1528–1535.
- Planque, B. and Fromentin, J.-M. (1996) *Calanus* and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.* **134**:101–109.
- Planque, B. and Reid, P.C. (1997) Changes in *Calanus finmarchicus* populations on a North Atlantic scale. *ICES CM 1997/T:01*, 1–7.
- Planque, B. and Reid, P.C. (1998) Predicting *Calanus finmarchicus* abundance from a climatic signal. *J. Mar. Biol. Assoc. UK* **78**:1015–1018.
- Reid, P.C. and Edwards, M. (2001) Long-term changes in the pelagos, benthos and fisheries of the North Sea. *Senckenbergiana Maritima* **32**:107–115.
- Reid, P.C. and Planque, B. (2000) Long-term planktonic variations and the climate of the North Atlantic. In: *The Ocean Life of Atlantic Salmon. Environmental and Biological Factors Influencing Survival*. D. Mills (ed.) Oxford: Fishing News Books, pp. 153–169.
- Reid, P.C., Surey-Gent, S.C., Hunt, H.G. and Durrant, A.E. (1992) *Thalassiothrix longissima*, a possible oceanic indicator species in the North Sea. *ICES Mar. Sci. Symp.* **195**:268–277.
- Reid, P.C., Battle, E.J.V., Batten, S.D. and Brander, K.M. (2000) Impacts of fisheries on plankton community structure. *ICES J. Mar. Sci.* **57**:495–502.
- Reid, P.C., Borges, M.F. and Svendsen, E. (2001a) A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fish. Res.* **50**:163–171.
- Reid, P.C., Holliday, N.P. and Smyth, T.J. (2001b) Pulses in eastern margin current with higher temperatures and North Sea ecosystem changes. *Mar. Ecol. Prog. Ser.* **215**:283–287.
- Reistad, M. and Iden, K.A. (1998) Updating, correction and evaluation of a hindcast data base of air pressure, winds and waves for the North Sea, Norwegian Sea and the Barents Sea. The Norwegian Meteorological Institute, Oslo. *Technical Report* **9**, 42 pp.
- Skogen, M.D. and Moll, A. (2000) Interannual variability of the North Sea primary production: comparison from two model studies. *Cont. Shelf Res.* **20**:129–151.
- Skogen, M.D. and Sjøiland, H. (1998) A user's guide to NORWECOM v2.0. The NORWegian ECOlogical Model system: Institute of Marine Research, Bergen. *Technical report Fiskeri og Havet* **18/98**, 42 pp.
- Skogen, M., Berntsen, J., Svendsen, E., Aksnes, D. and Ulvestad, K. (1995) Modelling the primary production in the North Sea using a coupled three-dimensional physical chemical biological ocean model. *Estuar. Cstl. Shelf Sci.* **41**:545–565.
- Skogen, M.D., Svendsen, E. and Ostrowski, M. (1997) Quantifying volume transports during SKAGEX with the Norwegian ecological model system. *Cont. Shelf Res.* **17**:1817–1837.
- Stigebrandt, A. (1980) Barotropic and baroclinic response of a semi-enclosed basin to barotropic forcing of the sea. In: *Proceedings of the NATO Conference on Fjord Oceanography*. H.J. Freeland, D.M. Farmer and C.D. Levings (eds). New York: Plenum Press, pp. 141–164.
- Svendsen, E., Fossum, P., Skogen, M.D. *et al.* (1995) Variability of the drift patterns of spring spawned herring larvae and the transport of water along the Norwegian shelf. *ICES C.M.* **1995/Q:25**.
- Svendsen, E., Berntsen, J., Skogen, M.D., Ådlandsvik, B. and Martinsen, E. (1996) Model simulation of the Skagerrak circulation and hydrography during SKAGEX. *J. Mar. Syst.* **8**:219–236.
- Sjøiland, H. and Skogen, M.D. (2000) Validation of a 3D biophysical model using nutrient observations in the North Sea. *ICES J. Mar. Sci.* **57**:816–823.
- Warner, A.J. and Hays, G.C. (1994) Sampling by the Continuous Plankton Recorder survey. *Prog. Oceanogr.* **34**:237–256.
- Woodruff, S.D., Slutz, R.J., Jenne, R.L. and Steurer, P.M. (1987) A comprehensive ocean-atmosphere dataset. *Bull. Am. Meteor. Soc.* **68**:1239–1250.