J. Mar. Biol. Ass. U.K. (2005), **85**, 435–450
Printed in the United Kingdom

Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries

Christopher P. Lynam*‡, Stephen J. Hay† and Andrew S. Brierley*

*Gatty Marine Laboratory, University of St Andrews, Fife, KY16 8LB, UK. †FRS Marine Laboratory, PO Box 101, Victoria Road, Aberdeen, AB11 9DB, UK. ‡Corresponding author, e-mail: cpl@st-and.ac.uk

Jellyfish medusae prey on zooplankton and may impact fish recruitment both directly (top-down control) and indirectly (through competition). Abundances of *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata* medusae (Scyphozoa) in the North Sea appear to be linked to large-scale inter-annual climatic change, as quantified by the North Atlantic Oscillation Index (NAOI), the Barents Sea-Ice Index (BSII) and changes in the latitude of the Gulf Stream North Wall (GSNW). Hydroclimatic forcing may thus be an important factor influencing the abundance of gelatinous zooplankton and may modulate the scale of any ecosystem impact of jellyfish. The population responses are probably also affected by local variability in the environment manifested in intra-annual changes in temperature, salinity, current strength/direction and prey abundance. *Aurelia aurita* and *C. lamarckii* in the north-west and south-east North Sea exhibited contrasting relationships to change in the NAOI and BSII: north of Scotland, where the North Sea borders the Atlantic, positive relationships were evident between the abundance of scyphomedusae (data from 1974 to 1986, except 1975) and the indices; whereas west of northern Denmark, a region much less affected by Atlantic inflow, negative relationships were found (data from 1973 to 1983, except 1974). Weaker negative relationships with the NAOI were also found in an intermediate region, east of Scotland, for the abundance of *A. aurita* and *C. capillata* medusae (1971 to 1982). East of Shetland, the abundance of jellyfish was not correlated directly with the NAOI but, in contrast to all other regions, the abundances of *A. aurita* and *C. lamarckii* (1971 to 1986, not 1984) were found to correlate negatively with changes in the GSNW, which itself was significantly positively correlated to the NAOI with a two year lag. On this evidence, we suggest that, for jellyfish, there exist three regions of the North Sea with distinct environmental processes governing species abundance: one north of Scotland, another east of Shetland, and a more southerly group (i.e. east of Scotland and west of northern Denmark). Impacts by jellyfish are likely to vary regionally, and ecosystem management may benefit from considering this spatial variability.

INTRODUCTION

The abundance of gelatinous zooplankton appears to be increasing in many marine ecosystems globally, and high abundances of jellyfish are hindering human activities from the Yangtze Estuary to the Black Sea and the Benguela (Brierley et al., 2001; Mills, 2001; Xian et al., 2005). The seasonal bloom of jellyfish medusae is a characteristic of many marine environments, but there is also great interannual variability in the abundance of medusae (Lynam et al., 2004; Purcell, 2005). When conditions are favourable, the biomass of jellyfish may bloom to unexpectedly high levels; for example, the population of *Aurelia aurita* in the Black Sea reached an estimated 300–500 million tons in the late 1980s (Mills, 2001). The fisheries by-catch of *Cyanea capillata* in the Yangtze Estuary increased from <1% of the total catch in 1998 to 85% in 2003, while in 2004 *Sanderia malayensis* bloomed for the first time and comprised 98% of the total catch (Xian et al., 2005). Jellyfish are important predators in marine ecosystems and may regulate the abundances of zooplankton and ichthyoplankton and thus impact fish recruitment (Purcell & Arai, 2001; Purcell, 2003; Lynam et al., in press). Interannual variation in jellyfish abundance will probably cause year to year variation in any impact of jellyfish on fish and ought to be considered in an ecosystem approach to fishery management.

The North Atlantic Oscillation (NAO) is the dominant mode of recurrent atmospheric variability over the North Atlantic. The NAO is quantified by an Index (NAOI) generated from the mean wintertime (December–March) difference in sea level pressure (SLP) between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland (Hurrell et al., 2003). The phase of the NAO (high/low) alters the prevailing wind field over northern Europe and influences atmospheric variables (i.e. wind speed and direction, air temperatures, heat and moisture transports, and precipitation) which lead to changes in sea temperature, salinity, river run-off, vertical mixing, and oceanic circulation. These factors, in turn, influence nutrient levels available for phytoplankton growth, and hence zooplankton production (Drinkwater et al., 2003). The timescales by which the oceanographic conditions respond to changes in the atmosphere vary. Surface temperatures and wind-driven currents change within days, whereas basin-scale ocean circulation may take many years to fully adjust to changes in atmospheric conditions (Reid et al., 1998). For example, it takes between two and three years for changes in the NAO to become evident in changes in the latitude of the Gulf Stream's 'North Wall' (GSNW) and in the coverage of sea-ice in the Barents Sea. The Gulf Stream travels eastwards from the USA coast near 33°N 75°W developing into the North Atlantic current at about 55°W, which drives Atlantic inflow into the North and Barents Seas. The high phase of the NAO, which strengthens westerly and trade winds, favours more northerly paths of, and transport by, the Gulf Stream and a reduced ice-coverage in the Barents Sea (Drinkwater et al., 2003) (Figure 1). The NAOI and GSNW strongly correlate with zooplankton abundance in the North Atlantic and North Sea (Drinkwater et al., 2003). In the period 1977 to 1979 the NAO was in a low phase (strongly negative index) and the North Sea suffered the coldest winters of the second half of the 20th Century. This same period saw high abundances of scyphomedusae (*Aurelia aurita* Lamarck, *Cyanea capillata* Lamarck, and *C. lamarckii* Péron & Lesueur) in the North Sea (Hay et al., 1990; Lynam et al., 2004). Further evidence for an NAO-driven influence on jellyfish abundance exists for Chesapeake Bay, where a low NAOI also results in a high abundance of *Chrysaora* scyphomedusae (Purcell & Decker, 2005; Purcell, 2005).

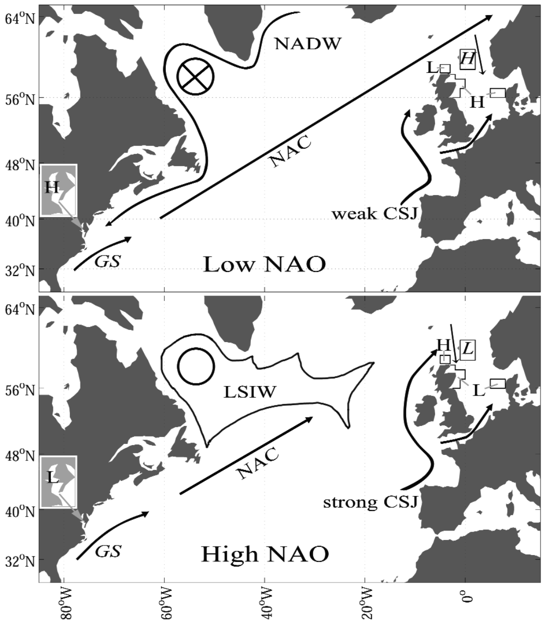

Figure 1. Schematic diagram of recognized NAO-governed changes in the strength of Atlantic currents, and possible controls on the abundance of jellyfish, adapted from Reid et al. (1998). NAC, North Atlantic Current; GS, Gulf Stream; CSJ, Continental Shelf Jet; LSIW, Labrador Sea Intermediate Water; NADW, North Atlantic Deep Water. Note that the changes in CSJ, LSIW, and NADW may require a prolonged period of high/low NAO influence. H/L signifies a relatively high/low jellyfish abundance in the defined rectangular regions, and italics indicate a two-year lag to NAO changes. Small arrows showing the shifting location of NAO-driven inflow to the northern North Sea are adapted from Planque & Taylor (1998). Chesapeake Bay relationship from Purcell & Decker (2005).

Hay et al. (1990) reported median abundances of medusae of *Aurelia aurita*, *Cyanea lamarckii* and *C. capillata* (Scyphozoa) between 1971 and 1986 in four defined regions of the North Sea, which were identified as the main areas of abundance of these species. The regions were north of Scotland (NoS), east of Shetland (ESh), east of Scotland (EoS) and west of northern Denmark (WND) (Figure 2). Lynam et al. (2004) used these data to examine possible climatic forcing of interannual variability via the NAOI. Significant inverse ($P<0.01$) relationships were found, with the median abundance of jellyfish (*A. aurita* WND, EoS and *C. lamarckii* WND) generally being high when the NAOI was low. The EoS dataset, however, contained an outlier that, when included in the regression of the abundance of *A. aurita* against the NAOI, rendered the relationship non-significant. We seek here to understand why that outlier existed in the EoS dataset and what implications it might have for our understanding of the possible climate-driven impact of jellyfish on the North Sea ecosystem. Lynam et al. (in press) showed that *A. aurita* medusae may affect detrimentally the recruitment of herring (*Clupea harengus*) in the North Sea, and that this

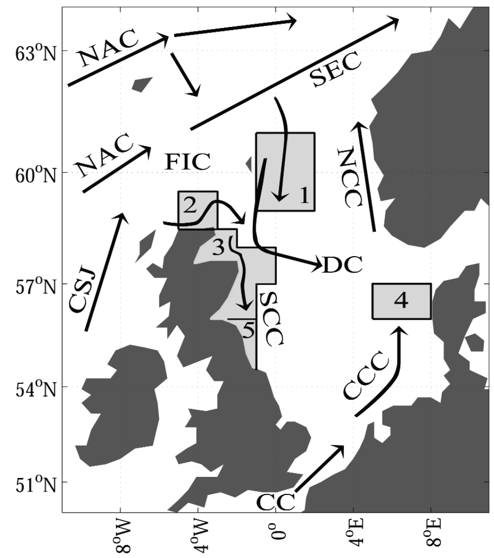

Figure 2. Map of survey area showing major currents, adapted from Holliday & Reid (2001), where region 1 is East of Shetland, 2 is North of Scotland, 3 is East of Scotland, 4 is West of northern Denmark, and region 5 is East of Northumberland. SEC, Shelf Edge Current; FIC, Fair Isle Current; DC, Dooley Current; SCC, Scottish coastal current; NCC, Norwegian coastal current; CCC, Continental coastal current; and CC, Channel current.

impact may be climatically mediated through the NAO and changes in the distribution and/or abundance of *C. capillata*. Here we also explore the role that jellyfish may have in driving the interannual variability in the recruitment and distribution of fish including plaice (*Pleuronectes platessa*) and salmon (*Salmo salar*), and the role that jellyfish may have as indicators of marine regime change.

MATERIALS AND METHODS

Medusa abundance data were collected between 1971 and 1986 (but not in 1984) during the routine summer International Council for the Exploration of the Sea (ICES) International 0-group Gadoid Surveys of the North Sea (Hay et al., 1990). Surveys were conducted using the International Young Gadoid Pelagic Trawl (IYGPT) and jellyfish (*Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata*) were a by-catch of these surveys. Trawls were conducted during June and July each year, and for the years 1971 and 1972 hauls were also made in August. From 2,030 IYGPT trawls throughout the North Sea in this period, more than 430,000 medusae were caught, identified and measured. Four regions were defined that were considered representative of the major areas of jellyfish abundance: east of Scotland; north of Scotland; east of Shetland and west of northern Denmark. Here we also consider a fifth region east of Northumberland in order to investigate the possible advection of medusae by the Scottish coastal current (Figure 2). A full description of survey methods is given in Hay et al. (1990) and Lynam et al. (2004).

Some errors were introduced to the jellyfish abundance data by the original data processing of Hay et al. (1990); medians of abundance were calculated initially for each grid square and these values were used to calculate the overall median abundance within the regions of interest. It would have been more robust to take directly the median of all catches located within each region. In each region mistakes were also made in allocating catches to positions, particularly in 1982 and 1983 in the east of Scotland region. Hence the median abundance values published by Hay et al. (1990) contain errors. Lynam et al. (2004) used these values for NAO analysis. In order to evaluate whether the NAO–abundance relationships found were real or merely an artefact of those errors, median abundances for all years and regions were recalculated here from the original catch records. The re-analysis additionally enabled maximum values of abundance to be calculated. The maximum abundance of medusae is a measure of the peak of the jellyfish bloom, which serves as a good indicator of interannual variability in jellyfish abundance in the North Sea; the median is a useful additional measure, particularly for *C. capillata* which does not form dense aggregations (Purcell, 2003). In addition, the use of the maximum abundance facilitated analyses for *A. aurita* and *C. lamarckii* in the region ESh since in most years their median abundance was zero. The mean abundance is not a statistically acceptable measure of abundance due to the great patchiness in jellyfish aggregations and hence the highly skewed (non-normal) range of densities.

Regression analysis was used to reassess links between medusa abundance and the North Atlantic Oscillation Index (NAOI). The winter (December–March) NAOI was obtained from the National Center for Atmospheric Research, Climate and Global Dynamics Division, Boulder, CO, USA, and monthly values were obtained from the University of East Anglia, Climatic Research Unit, Norwich, UK (Hurrell et al., 2003). The Gulf Stream North Wall (GSNW) and the Barents Sea-Ice Index (BSII) were also used in regression analyses; these indices incorporate the additional one- to two-year delayed impact of the NAO on the marine system, and together describe the strength and composition of inflowing water to the North Sea. Data for the annual mean of the 1st Principal Component of the GSNW (Taylor, 1995) were obtained from the Plymouth

Marine Laboratory, UK. The Barents Sea-Ice Index was supplied by the Institute of Marine Research, Bergen, Norway.

Interactions between medusae and commercial fish were also explored. Salmon landings in the central and northern North Sea were considered because the numbers of salmon caught have been linked to changes in northern hemisphere temperature and in zooplankton abundance, and jellyfish may be part of this relationship (Purcell & Sturdevant, 2001; Beaugrand & Reid, 2003). The abundance of plaice in the Thames Estuary has been negatively correlated with the NAOI (Attrill & Power, 2002) and plaice recruitment in the southern North Sea is a useful indicator of changes in Atlantic inflow through the English Channel (Wegner et al., 2003). Salmon landings for the central and northern North Sea were provided by ICES through Fishstat Plus version 2.3 2000 (FAO Fisheries Department, Fishery Information, Data and Statistics Unit) and plaice recruitment data for ICES Subarea IV (North Sea) were from ICES (ACFM report 2003).

Where necessary, medusa abundance data (median and maximum values) were natural logarithm transformed to normalize the variance of the distributions prior to further statistical analyses. Medusa abundance and the NAOI were also assessed for linear temporal trends, the significance of which was judged at the 0.05 level with a standard Student's *t*-test of the estimated slope parameter. Linear trends were removed in order to compare interannual variability between time-series. Linear regressions of abundance data against the environmental variables were made, for each species in each area, to compute models of the form:

$$y_t = ß_0 + ß_1.x_t + e_t \qquad (1)$$

where y_t was the natural logarithm of the medusa abundance value in year t, x_t was the value of the environmental variable in year t, e_t was an error term with unit variance and zero mean, and $ß_0$ and $ß_1$ were the intercept and slope parameters estimated using linear regression. Regressions with either fish recruitment or landings as the response variable (y) were also made against medusa abundance (eqn 1) and similarly multivariate regressions (with two predictors: x_1 total North Sea medusa abundance and x_2 the NAOI) were made using the linear regression feature in SigmaPlot® 2001 for Windows. Parameter significances for all models were assessed using a Student's *t*-test at the 0.05 level to minimize corresponding Type II error. The model assumptions (linearity, homogeneity of variance, normality and independence of residuals) were tested following procedures outlined in Krzanowski (1998). The Durbin–Watson (DW) statistic was used to assess residuals for first-order autocorrelation, and the Breusch–Godfrey test for higher-order serial correlation and the Shapiro–Wilk test was used to assess normality. Outliers were assessed using the mean shift outlier model: the largest absolute residual was tested using the t-distribution and the Bonferroni correction at the 0.05 significance level (Fox, 1997).

RESULTS

Jellyfish abundance

Linear trends with abundance increasing over time were detected in, and removed from, the median abundance data for *Cyanea capillata*: east of Shetland (ESh) (ln(median) r^2=0.55, P<0.01, N=15) and west of northern Denmark (WND) (median r^2=0.36, P<0.10, N=10); and for the combined abundance of all jellyfish species north of Scotland (NoS) (ln(median) r^2=0.57, P<0.10, N=11). In the area west of northern Denmark (WND), both the ln(maximum) and ln(median) abundance of *Aurelia aurita* and *Cyanea lamarckii* correlated significantly between species (Figure 3A,B). In the NoS region, a significant correlation was found between the median *C. lamarckii* and *C. capillata* medusa abundance (Figure 3C). The ln(median) *A. aurita* abundance correlated between the two regions east of Scotland (EoS) and WND, but only when the year 1983 was excluded did the regression satisfy the assumption of constant variances (Figure 3D).

Jellyfish and the winter (December–March) North Atlantic Oscillation Index

Significant regressions between jellyfish abundances and the winter NAOI were found in three of the five North Sea regions analysed (Figures 2, 4 & 5); positive regressions were found NoS and negative regressions EoS and WND (Table 1). Although the median abundance of *A. aurita* EoS observed in 1983 was higher than predicted by the regression with the NAOI (outside of the 95% CI bounds, Figure 4D), the recalculated value was not as high as previously reported by Hay et al. (1990).

Jellyfish and the monthly North Atlantic Oscillation Index

The complex phenomenon that is the NAO is often reduced to a dimensionless index, and it is assumed that if two years have the same value of the NAOI then there will be similar climatic influences exerted on the environment. However, no two NAO cycles are

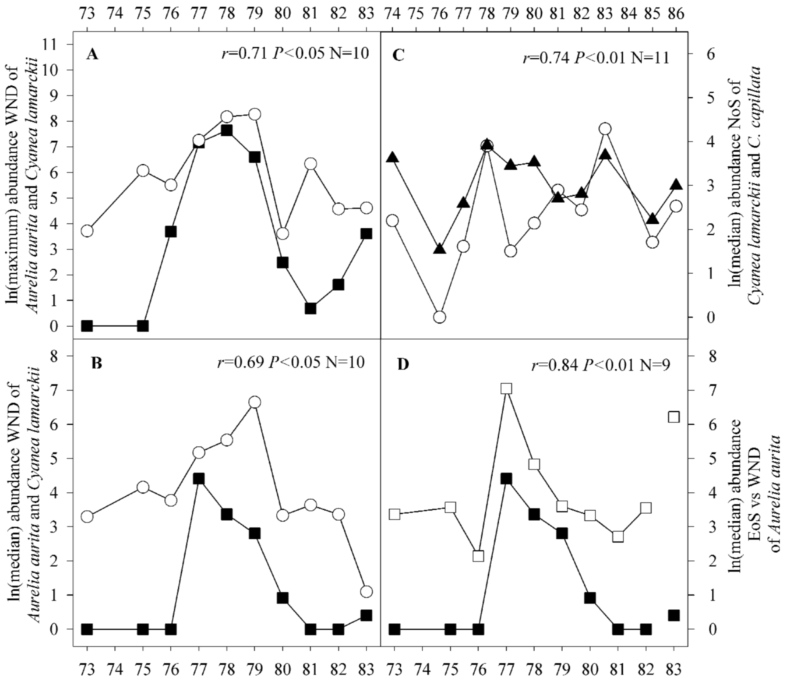

Figure 3. Interspecies correlations (showing Pearson correlation coefficients) for the abundance of *Aurelia aurita* and *Cyanea lamarckii* WND (A) ln(maximum) and (B) ln(median); (C) ln(median) *Cyanea lamarckii* and *Cyanea capillata* NoS. The inter-region relationship between *Aurelia aurita* ln(median) abundances EoS and WND is shown in (D). Note that the abundance of *Cyanea capillata* in (C) is 3+ln(median) for ease of visual comparison.

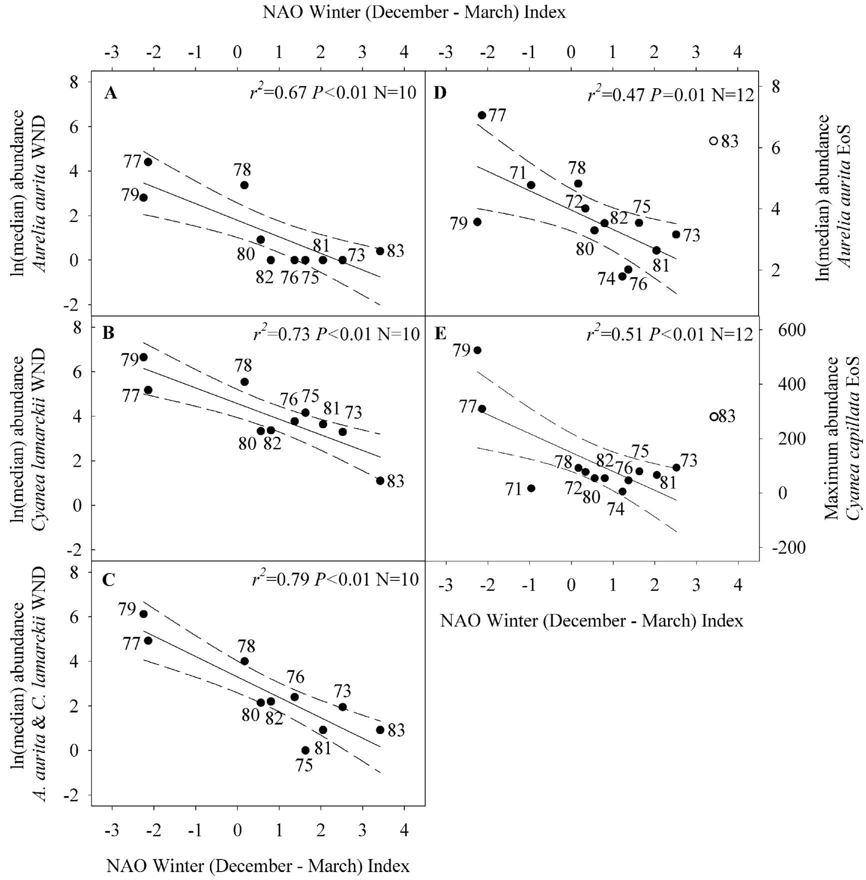

Figure 4. Regressions of median jellyfish abundance on the NAOI, left panels WND (A) *Aurelia aurita*, y=1.80-0.75x; (B) *Cyanea lamarckii*, y=4.57-0.70x; (C) for both species combined, y=3.30-0.92x ; and right panels EoS (D) *Aurelia aurita*, y=3.96-0.63x; and (E) *Cyanea capillata*, y=149-70x. All y-axis are ln(median) except (E) which is maximum abundance.

Table 1. *Significant linear regressions of maximum and median medusa abundances with the NAOI for three regions of the North Sea for* Aurelia aurita, Cyanea lamarckii, *and* Cyanea capillata *species of jellyfish.*

		r^2 for relationships between ln(median) medusa abundance and the NAOI							
Region	N	+/-	*A. aurita*	+/-	*C. lamarckii*	+/-	*C. capillata*	+/-	*A. aurita* & *C. lamarckii* combined
WND	10	-	0.67 ***	-	0.73 ***		n.s.	-	0.79 ****
EoS	12	-	0.47[a] **		n.s.		n.s.		n.s.
NoS	11		n.s.		n.s.		n.s.		n.s.

		r^2 for relationships between ln(maximum) medusa abundance and the NAOI							
Region	N	+/-	*A. aurita*	+/-	*C. lamarckii*	+/-	*C. capillata*	+/-	All species combined[b]
WND	10	-	0.51 **	-	0.43 **		n.s.	-	0.43 **
EoS	12		n.s.		n.s.	-	0.51[a, c] ***		n.s.
NoS	11	+	0.40[c] **	+	0.33 *		n.s.	+	0.52 **

N, number of observations; +/- indicates a positive or negative relationship between the variables; ****, $P<0.001$; ***, $P<0.01$; **, $P<0.05$; *, $P<0.10$; n.s., $P>0.10$.

Notes: [a], one year (1983) was excluded. [b], The regression WND is dominated by the regular high abundance of *C. lamarckii* and thus has an identical proportion of variability explained by the regression with *C. lamarckii* alone. The non-significant regression EoS merely replicates the *A. aurita* regression as *A. aurita* was most abundant EoS each year. [c], No ln transformation was necessary for the measure of abundance to fulfil the test for constant variance and was therefore not made.

the same and its monthly variation may result in subtly varying interactions with the marine environment. We plotted the monthly NAOI values grouped by phase for extremely low (1977 and 1979) and high (1973, 1975 and 1981) years and for 1983 (Figure 6A–C). In years of low NAOI, when jellyfish were most abundant east of Scotland and west of northern Denmark, the winter (December to March) NAOI showed an opposite monthly pattern to the years of high NAO when jellyfish were abundant north of Scotland (Figure 6A,B). We named the cycles Type I and II respectively. The NAO monthly cycle in the outlier year 1983 was expected to follow Type II, as the overall phase was high, and in December and January the cycle appeared to be an extreme form of Type II. However, in February and March the cycle reflected Type I (Figure 6C). We then created a difference index (March minus February) and used this in regressions of abundance in each area. Significant regressions were found for *A. aurita* medusae east of Scotland (EoS) and east of Northumberland (EoN) (Figure 6D–F). All regressions included all available years of the time-series and were significant with the unusual year 1983 included.

Jellyfish abundance, the Gulf Stream North Wall and the Barents Sea-Ice Index

A significant linear trend was removed from the GSNW index for the period 1971 to 1986 (r^2=0.39, $P<0.01$, N=16) so that the inter-annual variability in this time-series could be compared robustly to that in the jellyfish abundance data and NAOI. The detrended GSNW and the Barents Sea-Ice Index (BSII) were found to lag changes in the NAO by two years (once a linear trend was also removed from the NAOI 1969 to 1984 data, Figure 7A). Negative correlations were found for both the BSII and the detrended GSNW with the ln(maximum) abundance of medusae east of Shetland (ESh) (Figure 7). The BSII also correlated positively with medusa abundance north of Scotland and negatively west of northern Denmark (Figure 7D,F).

Cyanea capillata *and the recruitment of plaice*

Recruitment of plaice (*Pleuronectes platessa*) to age-1 was not found to be correlated with long-term changes in the spawning stock biomass (SSB) or landings for the period 1960–2000. Linear temporal trends over the period 1970–1986 (when jellyfish data are available) were evident in recruitment data of plaice (r^2=0.48, $P<0.01$, N=17) and also the landings data (r^2=0.65, $P<0.01$, N=17). Once detrended the recruitment data for 1973–1983 (no recruitment data for 1974) correlated with the median abundance of *C. capillata* WND (Figure 8A).

Atlantic salmon landings and jellyfish abundance

In the central and northern North Sea (ICES areas IVa and b), between 1971 and 1986, the landings of

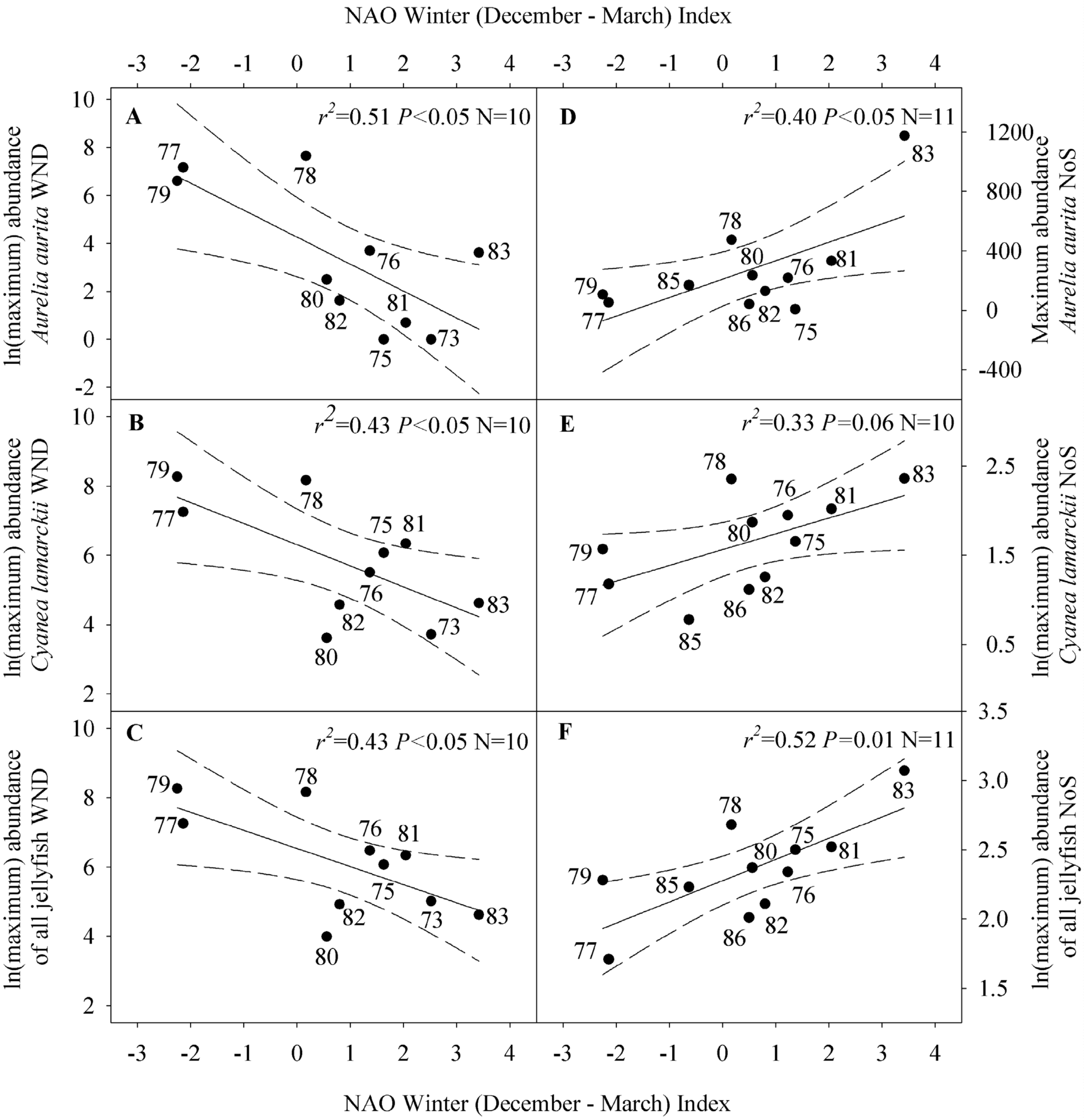

Figure 5. Regressions of maximum jellyfish abundance on the NAOI. Left panels WND (A) *Aurelia aurita*, y=4.26-1.12x; (B) *Cyanea lamarckii*, y=6.31-0.61x; (C) all species combined, y=6.54-0.52x. Right panels NoS (D) *Aurelia aurita*, y=209+124x; (E) *Cyanea lamarckii*, y=1.56+0.18x; (F) all species combined, y=2.28+0.15x. All y-axis are ln(maximum) except (D) which is maximum abundance.

salmon (*Salmo salar*), once detrended (linear negative trend; r^2=0.52, P<0.01, N=13), were positively correlated with the NAOI and negatively with the maximum abundance of *C. lamarckii* in the North Sea (Figure 8B). Sixty-eight per cent of the variability in salmon landings was explained by multivariate regression against both the NAOI and the maximum abundance of *C. lamarckii* (Figure 8B). Although the maximum abundance of all jellyfish, or of *Aurelia aurita* only, did not significantly correlate with salmon landings when modelled as the sole explanatory variable, both measures of abundance did significantly correlate when the NAOI was included as an additional explanatory variable (r^2=0.69 and P=0.003 for both models).

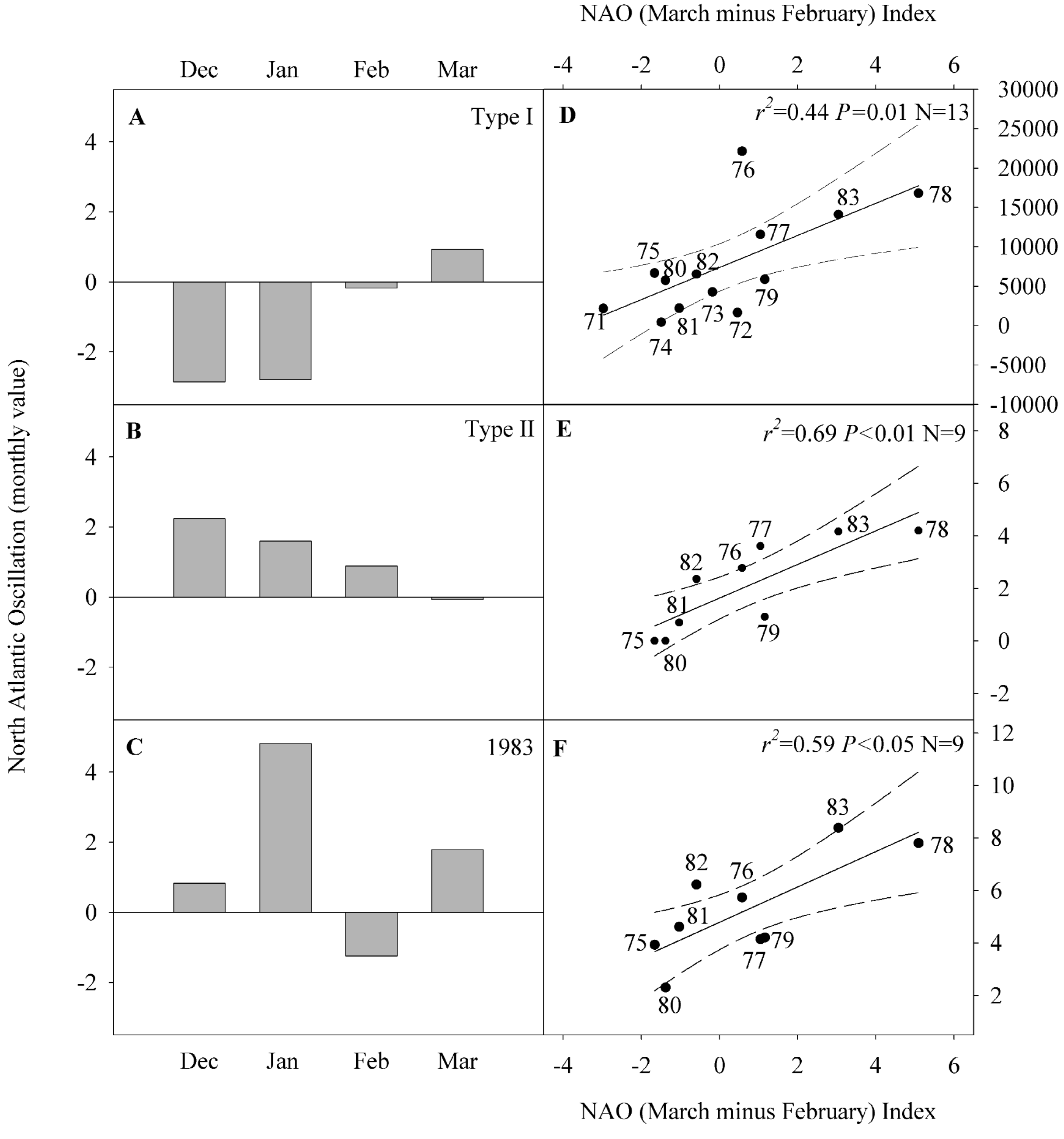

Figure 6. Monthly patterns in NAO winter index, (A) is Type I for the low NAO years 1977 and 1979; (B) is Type II for 1973, 1975 and 1981; and (C) is the NAO for 1983, where Type I/II corresponds to high/low median abundance of jellyfish EoS and WND and the outlier year appears as a combination of both types. (D–F) Response by *Aurelia aurita* to the NAO (March–February) Index: east of Scotland (D, maximum *A. aurita* abundance including all years, y=7372+2037x) and east of Northumberland (E ln(median), y=1.63+0.64x, and F ln(maximum) *A. aurita* abundance, y=4.79+0.67x).

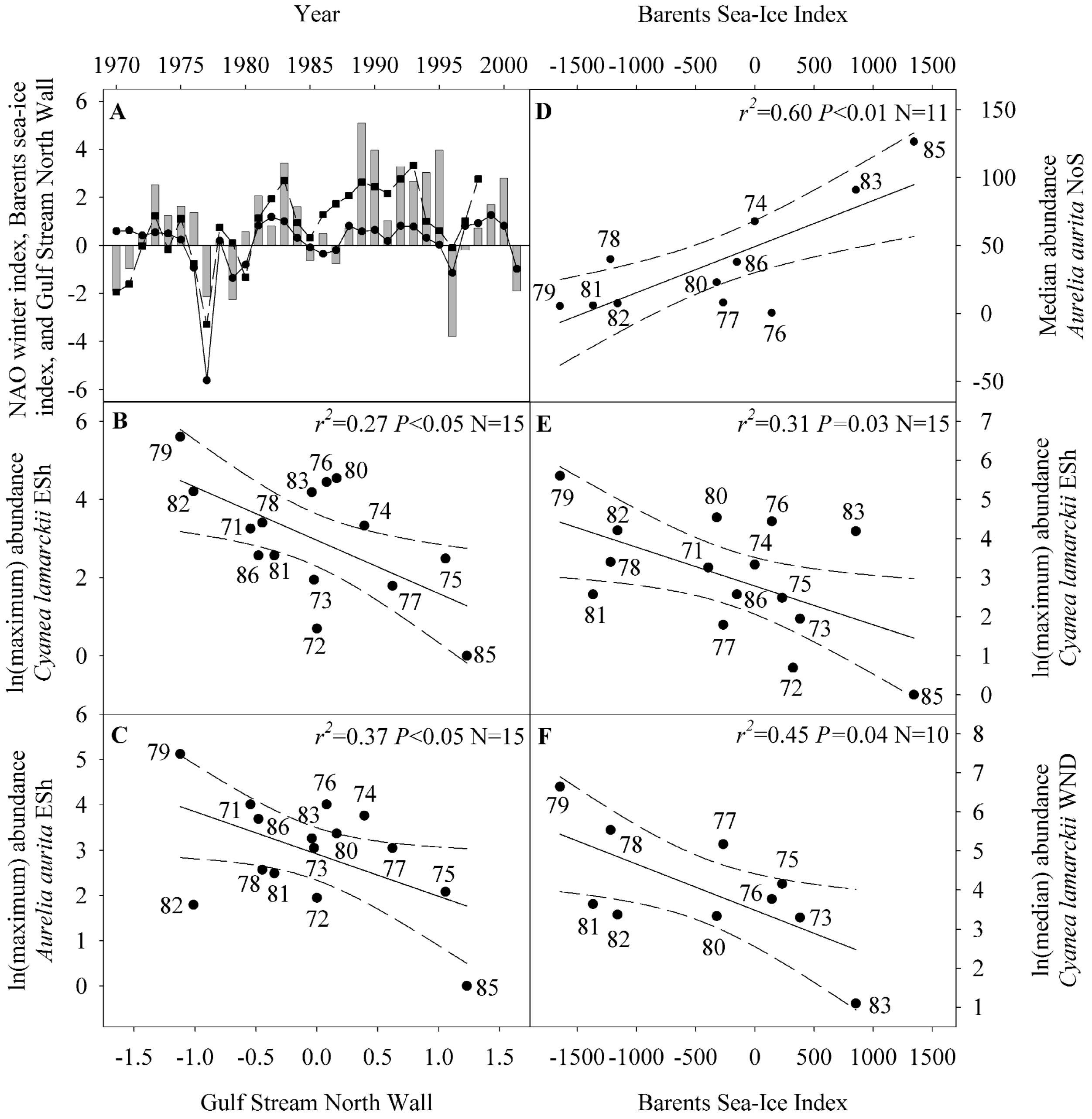

Figure 7. (A) The NAO winter index (bars) for 1970–2001 with the (detrended) Gulf Stream North Wall (GSNW squares and dashed line, correlation with NAO 1970–1998 r^2=0.37, P<0.01, N=29 and 1971–1986 r^2=0.46, P<0.01, N=16) and the Barents Sea-Ice Index (BSII, circles and line, correlation with NAO 1970–2001 r^2=0.23, P<0.01, N=32 and 1971–1986 r^2=0.34, P=0.02, N=16) both lagged by two years relative to the NAO. When positive, the NAO has a warming effect on the North Sea and two years later the Gulf Stream follows a more northerly path and the Barents Sea has reduced ice coverage. (B–C) are regressions of ln(maximum) jellyfish abundance east of Shetland against the GSNW, B: *Cyanea lamarckii*, y=2.96-1.36x, C: *Aurelia aurita*, y=2.91-0.93x. (D–F) are regressions of jellyfish regional abundance against the BSII, D: *Aurelia aurita* north of Scotland, y=49.3+0.04x; E: *Cyanea lamarckii* ln(maximum) abundance east of Shetland, y=2.79-0.001x, and F: *Cyanea lamarckii* ln(median) abundance west of northern Denmark, y=3.49-0.001x.

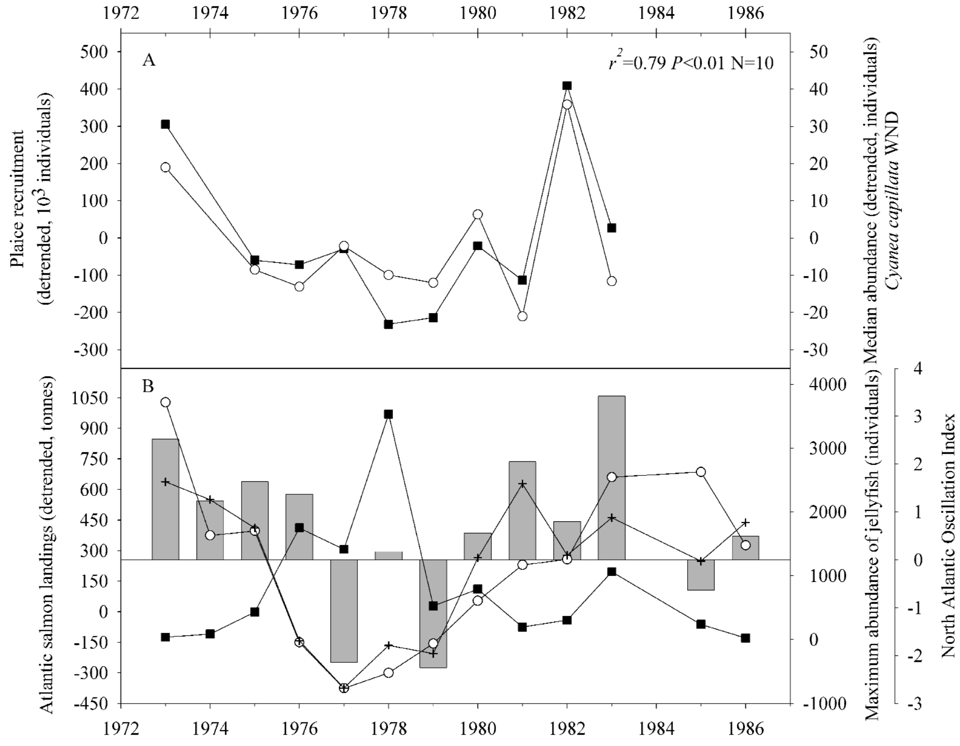

Figure 8. (A) Correlation between plaice recruitment (open circles and solid line) in the southern North Sea and *Cyanea capillata* abundance west of northern Denmark (squares and solid line). (B) Time-series of salmon (*Salmo salar*) landings in the central and northern North Sea (open circles and solid line), the maximum abundance of *Cyanea lamarckii* medusae (squares and solid line) and the NAO (bars) showing the modelled salmon landings (crosshairs and solid line; correlation with detrended landings: r^2=0.68, P<0.01, N=10, $y=321-0.23x_1-134x_2$, where x_1 is the maximum abundance of *Cyanea lamarckii* and x_2 is the NAO. Pearson correlation coefficients between salmon landings and: the NAOI *r*=0.62, *P*=0.02, N=13; the maximum abundance of *C. lamarckii* *r*=-0.63, *P*=0.02, N=13.

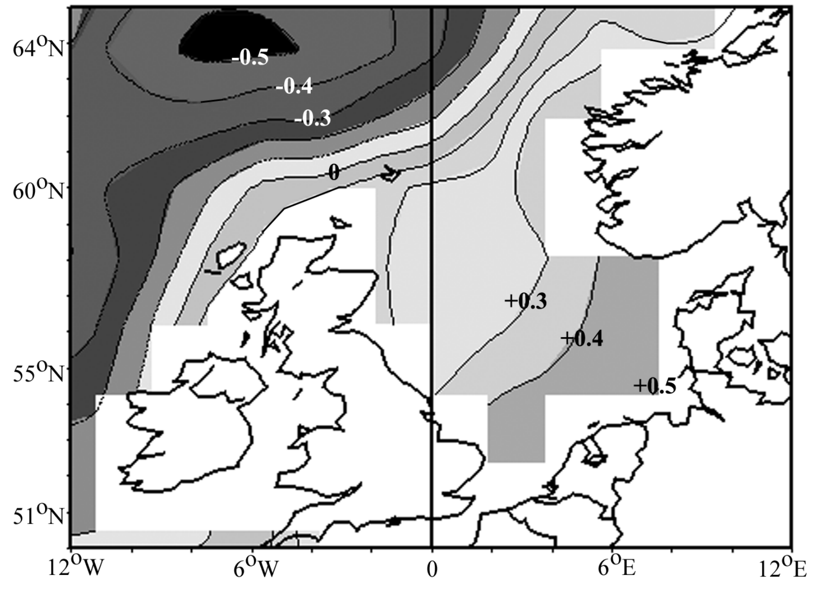

Figure 9. Geographic pattern of correlations between the NAO winter index (December to March) and SST (March to June) in the North Sea for the period 1948–2003. Produced using NCAR/NCEP Reanalysis Project www.cdc.noaa.gov (Kalnay et al., 1996).

DISCUSSION

Jellyfish and the NAO

This analysis has reaffirmed our previous finding that jellyfish abundance in the North Sea is linked to the climate, as quantified by the North Atlantic Oscillation Index (NAOI). Furthermore, the investigation of maximum abundance of medusae has revealed a population of jellyfish north of Scotland (NoS) that shows an opposite response to the NAO-driven environmental change relative to jellyfish populations in the regions east of Scotland (EoS) and west of northern Denmark (WND). The spatial variability shown by the relationship between jellyfish abundance and the NAOI do not falsify our hypothesis that the climate is a primary factor influencing jellyfish abundance, in fact it supports it (Drinkwater et al., 2003). The pattern of spatial variability is consistent with the pattern found in the strength of correlations between the NAOI and sea surface temperature (SST) (Figure 9). Salinity in the shallow, south-eastern North Sea is affected greatly by NAO-related precipitation. Whereas, in the deeper, colder waters of the northern North Sea (NoS and ESh) salinity is influenced primarily by oceanic inflow. The region WND includes an amphidromic point, which may serve to aggregate medusae. We suggest that, of the five regions studied (Figure 2), the region WND is the most isolated from external oceanic influences, which reduces the likelihood of species migrations, and enhances the relationship between jellyfish abundance and the climate.

East of Shetland: the North Atlantic Current influence on jellyfish abundance

The Gulf Stream North Wall (GSNW) and the Barents Sea-Ice Index (BSII) were negatively related to the abundance of medusae ESh (Figure 7). Wintertime Atlantic inflow ESh is also significantly negatively correlated with the NAO (Planque & Taylor, 1998). So, it appears that longer term changes (of the order of two years) in the composition and/or flow rate of the North Atlantic Current may exert a stronger influence on jellyfish abundance ESh than do concomitant changes in the NAO. Together the relationships imply that it is the negative phase of the NAO that is favourable to jellyfish abundance ESh, as it is EoS and WND, but in this high flow region the integrating effect of the ocean on the atmospheric variability appears to delay the impact on jellyfish abundance.

North of Scotland: the contrasting response of jellyfish to the NAO and the influence of the North Atlantic Current and the Continental Shelf Jet (CSJ)

The mixed advective region NoS is located on a boundary of the North Sea and Atlantic Ocean. We can see from a NAO–SST correlative map (Figure 9) that the region NoS occupies the intermediate area between positive and negative correlations between the NAO and SST (in agreement with Planque & Taylor, 1998). In contrast to the inflow in the region ESh, the inflow NoS by the Fair Isle current during the winter is significantly positively correlated with the NAO (Planque & Taylor, 1998). Interestingly the temperature and the current flow measured in the Svinvøy section (that runs north-west from 62°N on the Norwegian coast to 64°40'N) of the Faeroe–Shetland Channel is also positively correlated with the NAO (Mork & Blindheim, 2000; Orvik et al., 2001). Positive relationships between medusae abundance and both the NAOI and the BSII (high abundance in years of low ice coverage) were found (Figures 5D–F & 7D) indicating that the environmental conditions NoS are different from elsewhere in the North Sea and/or that changes in the NAO are manifest in differing environmental effects.

Interacting oceanographic influences

The high NAO conditions in the 1990s have been associated with a weak North Atlantic Current, a strong Continental Shelf Jet (Reid et al., 1998) and a strong inflow via the Fair Isle Current through the region NoS (Planque & Taylor, 1998) (Figure 1). Assuming this relationship held during the jellyfish survey period (1971–1986), the high medusae abundances seen NoS under high NAO conditions, and WND/EoS under low NAO conditions, imply that a strong Continental Shelf Jet and weak North Atlantic Current resulted in increased advection to the NoS region of oceanic water, whereas the reverse resulted in elevated advection to more southerly areas of the North Sea. Modelling has shown that during the first three months of the year the NAOI is related to overall Atlantic inflow to the northern North Sea (including flow from both the North Atlantic Current and the Continental Shelf Jet); for water between 0 and 150 m deep the NAO is positively correlated with inflow, while for deeper water (150–500 m, that largely derives from the Norwegian trench) the NAOI is negatively correlated with inflow (Reid et al., 2003). So the opposite relationship, between jellyfish abundance and the NAO, prevailing NoS relative to WND could also be due to changes in the depth-origin of inflowing water.

1983, the transport of medusae NoS/ESh to EoS/EoN, and the NAO monthly pattern

Using the newly recalculated jellyfish abundance data, 1983 was no longer a statistical outlier in the relationship between jellyfish abundance and the

NAOI (Bonferroni corrected $P>0.10$) even though it was an outlier year in the regression of *Aurelia aurita* abundances between the regions EoS and WND (Figure 3D). However, 1983 was still the most influential year (Cook's distance 0.6 for 1983, all others <0.2) and the inclusion/exclusion of this year results in a non-significant/significant regression of ln(median) *Aurelia aurita* abundance EoS, and also of maximum *Cyanea capillata* abundance EoS, against the NAOI (Figure 4D,E). 1983 was clearly an unusual year.

Although the interannual variability in abundance of *A. aurita* in the regions EoS and WND was largely in phase, a separate Atlantic influence may drive dynamics EoS by advecting medusae, nutrients, and/or prey into the region from more northern areas (Figures 3D & 6) (Frid & Huliselan, 1996). In 1983 a late-summer inflow of a large body of Atlantic water was deemed to have forced the migration of herring from their northern spawning grounds (near the Orkneys and west of the Shetland Isles) to Aberdeen Bank in the Buchan region EoS, from where they had been absent for the previous 16 years (Corten, 1999a). However, herring larvae were found in each of the years 1971–1986 in the Buchan region EoS and their abundance positively correlated with that of *A. aurita* ($r=0.66$, $P<0.05$, N=10), suggesting that both herring larvae and medusae are advected into the region (Lynam et al., in press). Inspection of the spatial distribution of the median abundance of medusae revealed that only during 1983 were medusae of both *A. aurita* and *C. capillata* abundant in the Fair Isle current (between the three regions EoS, NoS and ESh) indicating that this may be the principal source of Atlantic water inflow (Figure 2). The Fair Isle current flows south into the Scottish coastal current toward the Northumberland coast and also into the Dooley current that sweeps into the central North Sea, i.e. the two areas where medusae were also unusually abundant in 1983.

Two copepod species, *Candacia armata* and *Metridia lucens*, that are Atlantic water indicators were also found in high abundance during 1983 off the coast of Northumberland in Continuous Plankton Recorder (CPR) data (Evans & Edwards, 1993). Analysis here of CPR data (obtained from D. Stevens of SAHFOS) for the east of Scotland region, found that 75% and 79% of the total CPR catch between 1971 and 1986 of *C. armata* and *M. lucens* respectively was found in 1983. Corten (1999b) created an index of the combined abundance of *C. armata* and *M. lucens* and found that between 1965 and 1982 the index was lower than its mean for the period 1948 to 1996, but in 1983 the index rose to a value higher than the mean for the first time in 19 years. The low period of the *Candacia/Metridia* index corresponded to a declining period of the abundance of mackerel (*Scomber scombrus*, an Atlantic fish species) in the north-western North Sea, and a period of increased abundance of sprat (*Sprattus sprattus*, a neritic species) indicating that inflow during this time was relatively low (Corten, 1999b). Therefore the direct air–sea influence of the NAO may have been dominant prior to 1983. Beaugrand et al. (2002) defined biogeographic groups of Calanoid copepods and found that the number of southern shelf edge species and of psuedo-oceanic temperate species increased north and east of Scotland after 1983; they suggested that they had been brought into the North Sea from the Atlantic via the Continental Shelf Jet.

1983 was also an unusually warm year, a high temperature anomaly (greater than any value between 1977 and 1988) was found at the Norwegian coastal station, Utsira (Furnes, 1992), and in the Svinvøy section of the Faeroe–Shetland Canal (Mork & Blindheim, 2000). Mork & Blindheim (2000) showed that in summer 1983 the warm offshore waters (200 to 350 km) of the Svinvøy section were restricted to the surface (<150 m deep), while in the low NAO year 1987 warm waters penetrated much more deeply (between 200 and 500 m deep). This difference in the association of deep and shallow water temperature with the NAO mirrors the changing influence of the NAO on inflow to the North Sea (Reid et al., 2003). Reduced sea-ice cover in the Barents Sea in 1983 indicate that warm, saline waters (i.e. Atlantic) penetrated both the North and Barents Seas. Since 1983 was the fourth consecutive high NAO year we would expect that this water was due to a strong CSJ and that this, combined with the switch in the NAO monthly cycle to Type I, elevated the SCC so that nutrients, prey and/or medusae were advected EoS (Figure 2). This may explain the outlier year (1983) found in the winter NAOI–*A. aurita* correlation EoS.

The highly positive or negative values of the NAO between December and February largely determine whether or not the overall winter (December–March) NAO index is positive or negative. Therefore we hypothesize that the NAO in these months determines the principal impact for jellyfish on the environment and that the subsequent switching of the cycle in February and March could result in a distinct, secondary influence.

The difference between the March and February NAOI monthly values may be more predictive of jellyfish abundance EoS and EoN than the overall phase of the winter index. All regressions between *A. aurita* abundance EoS and EoN against the NAO (March–February) difference index were positive, therefore when the March NAO value is much greater than the

February NAO value high abundances are expected EoS and EoN. This implies that a Type I NAO cycle, particularly during February and March, is favourable to medusae in these areas. This agrees with the negative regressions against the winter NAO found EoS and WND, since negative NAO years generally had a Type I cycle. Between January and April, *A. aurita* ephyrae are being liberated from the benthic scyphistomae and dispersed by advection, so wind-driven currents governed by the NAO may be particularly important for jellyfish during this period.

It appears that the NAO winter index can be considered in two ways in terms of its effect on jellyfish abundance. Firstly the overall phase (high/positive or low/negative) of the cycle, and secondly the monthly evolution and phase switch between February and March. The overall phase is the dominant driving force on the North Sea; however, a weaker secondary force may exist. During the summer, the north Atlantic pressure dipole becomes much weaker and the immediate effect of the NAO on the North Sea conditions (e.g. temperature and inflow) becomes non-significant. However, the earlier winter/spring influence has a lasting impact that continues to be evident in the summer months. The final phase of the cycle in March, which is often opposite to the overall phase, may exert a significant secondary force on wind-driven currents (such as the SCC) and on the resulting marine environment during the summer. The combination of the two forces: the primary (overall phase of the December–March index) and secondary (February to March switch) appears to explain the spatial variability between the jellyfish abundance–NAOI relationships.

West of northern Denmark, where the direct air–sea effects are the primary driving factors, the overall phase of the NAOI is strongly correlated with the abundance of medusae. In the intermediate region east of Scotland the primary influence of the NAOI is significantly correlated with the abundance of medusae if the extreme year 1983 is excluded. This year appears to be influenced by a late inflow of Atlantic water and the secondary March–February NAO index accounts for this. The waters north of Scotland (NoS) appear to be in an 'Atlantic regime', in contrast to the 'North Sea regime' west of northern Denmark (WND), and the abundance of jellyfish NoS shows the expected opposite response, relative to jellyfish abundance WND, to the primary influence of the NAOI and the BSII. The region east of Shetland is in the area of major oceanic inflow to the North Sea and as such the jellyfish abundance is correlated not with the direct (primary or secondary) influence of the NAO but with the delayed response of the Gulf Stream and the BSII, indicating that the North Atlantic current is the dominant influence here.

Similar spatial variability in the response of crustacean and gelatinous zooplankton to environmental change

Beare et al. (2002) reported a north-west/south-east divide in the response of zooplankton abundance to salinity, temperature, and stratification changes in the North Sea. Our finding of contrasting responses by jellyfish to the NAOI are consistent with their analysis. For the north-western North Sea, Beare et al. (2002) found salinity to be correlated positively with abundance of *Calanus finmarchicus* (a northern boreal species) and negatively with an index of abundance of temperate Atlantic taxa (*Centropages typicus*, *Calanus helgolandicus* and *Candacia armata*); the opposite was found in the south-east. Beare et al. (2002) suggested the temperate Atlantic taxa were most likely brought into the northern North Sea via the CSJ inflow (NoS) that feeds the Fair Isle Current, in agreement with Beaugrand (2002) (Figure 2). In contrast, Beare et al. (2002) argued that *Calanus finmarchicus* is brought into the North Sea via the North Atlantic Current (flowing ESh). The switch between high abundance of *Calanus finmarchicus* and of *C. helgolandicus* in the North Sea has been shown to be correlated with the NAO (Planque & Taylor, 1998). The advection of *C. finmarchicus* into the North Sea from its overwintering area in the deep Shetland canal mirrors that of the change in distribution of jellyfish abundance in the North Sea. Years of high NAOI result in a more northern distribution and low NAOI years a more southern distribution of jellyfish and *C. finmarchicus*.

Pelagic–benthic community coupling

Scyphozoan jellyfish have both benthic (scyphistomae) and pelagic (medusae) stages. Changes in the abundance of medusae in the North Sea might be due to an impact by hydroclimatic factors on the benthic or the pelagic stage, or on both. We have emphasized the effect of climate on the distribution of medusae, but changes in prey levels and other environmental effects could lead to the observed changes in the abundance of medusae, possibly through increased strobilation (Purcell, 2005; Lynam et al. 2004). The warm sea temperature in 1983 may also have contributed to the extremely high medusa abundance, since high temperatures can increase the rate of strobilation and ephyrae production (Purcell et al., 1999).

A shift in the community composition of the plankton between 1979 and 1980 (identified in CPR data for 1973 to 1988) in the eastern North Sea (CPR area C1, which includes the region WND) but not the western North Sea was reported by Austen et al. (1991). A shift delayed by one year in the benthos in the Skagerrak and also off the coast of Northumberland was also reported, indicating that the pelagic and benthic communities in the eastern, but not the western, North Sea are linked (Austen et al., 1991). The time lag of the benthic shift was attributed to the slow reproductive rates of the benthic species relative to the plankton. Austen et al. (1991) noted that the plankton east of Northumberland is influenced strongly by Atlantic Water inflow, and they suggested that this might explain the difference in the strength of the pelagic–benthic coupling there. We have similarly suggested that the rate and composition of Atlantic water inflow to the North Sea may explain the observed deviations of *Aurelia aurita* abundance from the NAO relationship east of Scotland and Northumberland. If the benthic communities are indeed linked, then we may hypothesize that the NAO-related changes in the North Sea alter strobilation (during January–April) of the scyphistomae both EoS and WND, and that the response WND is greatest due to the minimized effects of Atlantic water on the pelagic stage there.

The contrasting response of jellyfish abundance NoS to the NAOI may also be explained by the response of benthic scyphistomae. Dippner & Kroncke (2003) report a positive relationship between the NAOI and macrozoobenthos abundance and biomass in the southern North Sea in spring between 1978 and 1999. Tunberg & Nelson (1998) found significant ($P<0.05$) positive and negative correlations between the NAOI and macrobenthic community biomass along the Swedish west coast. Correlations were negative inshore and at a deep (300 m) station but positive at two mid-depth (50 and 100 m) stations. Therefore the location and depth of scyphistomae may be important in determining the response of jellyfish production to environmental changes associated with the NAO.

Plaice age-1 recruitment and Cyanea capillata *medusae*

The positive correlation between the abundance of jellyfish WND and the recruitment success of plaice indicates that much of the interannual variation in both species is driven by similar changes in the hydroclimatic environment. However, WND neither measure correlates with the NAOI. The abundance of plaice in the Thames Estuary has been shown to be negatively correlated with the NAOI (Attrill & Power, 2002), which is similar to the relationship found here between *C. capillata* abundance EoS and the NAOI. Wind-induced currents and the intrusion of Atlantic water into the North Sea via the English Channel may combine to advect plaice eggs and larvae towards their nursery grounds along the Dutch, German and Danish coasts (Wegner et al., 2003). At times, *C. capillata* is also highly abundant WND and may be influenced by similar advective processes.

Although the positive correlation between plaice recruitment and *C. capillata* abundance indicates that there is no significant predatory impact on the fish population by jellyfish, this does not mean that *C. capillata* do not inflict some mortality on plaice eggs and larvae. *Aurelia aurita* has been recorded consuming newly hatched plaice at a hatchery in Port Erin (Irish Sea) (Russell, 1970), and plaice larvae have been shown by Bailey & Batty (1984) to be highly susceptible to predation by these medusae. The larger *C. capillata* medusae, with greater surface area than *A. aurita* and many more and longer tentacles, may be a more successful predator on plaice than *A. aurita*. Plaice spawn between mid-December to early March in the southern and central North Sea and the larvae may spend up to three months in surface waters before reaching the near-shore nursery areas (Wegner et al., 2003). *Cyanea capillata* ephyrae may appear from February onwards, small medusae are present in April and May, while larger medusae are commonly found between June and October and very large animals may even overwinter. Even small *C. capillata* may consume fish eggs and larvae (Purcell & Arai, 2001), and these jellyfish may prey on those plaice eggs and larvae that are spawned toward the end of the season in the area WND and also on those that are swept in the circulation currents from their spawning grounds further south.

Salmon landings and Cyanea lamarckii *medusae*

The inverse relationships found here between *C. lamarckii* abundance and salmon landings are unlikely to indicate a direct negative impact by these relatively small medusae on adult fish. However, pink salmon (*Oncorhynchus gorbuscha*) and *C. capillata* in Prince William Sound, Alaska, have been shown to be potentially direct competitors, particularly for larvacean prey (Purcell & Sturdevant, 2001). A high abundance of jellyfish in the North Sea, or perhaps a negative NAOI, may indicate poor local conditions for feeding by salmon, resulting in an early/strong migration northwards to feeding grounds in the Norwegian and Greenland Seas and thus lower landings.

Jellyfish are highly abundant during the summer, particularly in coastal areas of the North Sea, so it is likely that salmon post-smolts may come into close proximity with jellyfish swarms as soon as they emerge from the rivers. Dense swarms of jellyfish (including *A. aurita* and *Cyanea* spp.) have been particularly damaging to farmed salmon. When small medusae and nematocysts shed from larger animals have passed though the cages/nets they have caused severe lesions in, and death of, thousands of farmed salmon (Båmstedt et al., 1998). In the wild, fish may actively avoid jellyfish (Xian et al., 2005), so dense and widespread aggregations of medusae in the North Sea may encourage the migration of the fish northwards. Therefore the low landings when jellyfish abundances are high might be due in part to active avoidance of the jellyfish, and of resulting food-impoverished areas, by the salmon. Alternatively jellyfish abundance may be high due to an absence of salmon. Catches of Atlantic salmon in the North Sea have been found to be negatively related to northern hemisphere temperatures in the years 1966 to 2000 (Beaugrand & Reid, 2003). Therefore it is also possible that both salmon landings and the abundance of *C. lamarckii* have changed with the environment.

Concluding remarks

Further study is required to explore the aforementioned and other possible effects of jellyfish on North Sea fisheries. Ecosystem based analyses of the marine environment should be conducted in order to examine the regulatory role of medusae on zooplankton abundance and fish recruitment, and the regional impact of jellyfish ought to be considered in ecosystem management schemes.

We are grateful to J. Hurrell for making the NAOI data freely available at http://www.cgd.ucar.edu/~jhurrell, A. Taylor for the GSNW data http://www.pml.ac.uk/gulfstream/, K. Gjertsen and H. Loeng for the Barents Sea-Ice Index data. We would like to thank J. Purcell and an anonymous referee for their constructive criticisms on the initial draft of this paper.

C.P.L. was funded by the Natural Environment Research Council, UK.

REFERENCES

Attrill, M.J. & Power, M., 2002. Climatic influence on a marine fish assemblage. *Nature, London*, **417**, 275–278.

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

Bailey, K.M. & Batty, R.S., 1984. Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring - development and vulnerability to capture. *Marine Biology*, **83**, 287–291.

Båmstedt, U., Fossa, J.H., Martinussen, M.B. & Fosshagen, A., 1998. Mass occurrence of the physonect siphonophore *Apolemia uvaria* (Lesueur) in Norwegian waters. *Sarsia*, **83**, 79–85.

Beare, D.J., Batten, S., Edwards, M. & Reid, D.G., 2002. Prevalence of boreal Atlantic, temperate Atlantic and neritic zooplankton in the North Sea between 1958 and 1998 in relation to temperature, salinity, stratification intensity and Atlantic inflow. *Journal of Sea Research*, **48**, 29–49.

Beaugrand, G. & Reid, P.C., 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, **9**, 801–817.

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

Brierley, A.S., Axelsen, B.E., Buecher, E., Sparks, C.A.J., Boyer, H. & Gibbons, M.J., 2001. Acoustic observations of jellyfish in the Namibian Benguela. *Marine Ecology Progress Series*, **210**, 55–66.

Corten, A., 1999a. The reappearance of spawning Atlantic herring (*Clupea harengus*) on Aberdeen Bank (North Sea) in 1983 and its relationship to environmental conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 2051–2061.

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

Dippner, J.W. & Kroncke, I., 2003. Forecast of climate-induced change in macrozoobenthos in the southern North Sea in spring. *Climate Research*, **25**, 179–182.

Drinkwater, K.F. et al., 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. In *The North Atlantic Oscillation: climatic significance and environmental impact* (J. W. Hurrell et al.), pp. 279. Washington DC: Geophysical Monograph Series, American Geophysical Union.

Evans, F. & Edwards, A., 1993. Changes in the zooplankton community off the coast of Northumberland between 1969 and 1988, with notes on changes in the phytoplankton and benthos. *Journal of Experimental Marine Biology and Ecology*, **172**, 11–29.

Fox, J., 1997. *Applied regression, linear models, and related methods.* Thousand Oaks, London: Sage.

Frid, C.L.J. & Huliselan, N.V., 1996. Far-field control of long-term changes in Northumberland (NW North Sea) coastal zooplankton. *ICES Journal of Marine Science*, **53**, 972–977.

Furnes, G.K., 1992. Climatic variations of oceanographic processes in the north European seas - a Review of the 1970s and 1980s. *Continental Shelf Research*, **12**, 235–256.

Hay, S.J., Hislop, J.R.G. & Shanks, A.M., 1990. North-Sea scyphomedusae - summer distribution, estimated biomass and significance particularly for O-group gadoid fish. *Netherlands Journal of Sea Research*, **25**, 113–130.

Holliday, N.P. & 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 Journal of Marine Science*, **58**, 270–274.

Hurrell, J.W., Kushnir, Y., Ottersen, G. & Visbeck, M., 2003. An overview of the North Atlantic Oscillation. In *The North Atlantic Oscillation: climatic significance and environmental impact* (ed. J.W. Hurrell et al.), pp. 1–35. Washington DC: Geophysical Monograph Series, American Geophysical Union.

ICES, 2003. *Report of the ICES advisory committee on fish management 3.5.6.* Copenhagen: ICES.

Kalnay, E. et al., 1996. The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society*, **77**, 437–471.

Krzanowski, W.J., 1998. *An introduction to statistical modelling.* London: Arnold.

Lynam, C.P., Hay, S.J. & Brierley, A.S., 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography*, **49**, 637–643.

Lynam, C.P., Heath, M.R., Hay, S.J. & Brierley, A.S., in press. Evidence for impacts by jellyfish on North Sea herring recruitment. *Marine Ecology Progress Series.*

Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*, **451**, 55–68.

Mork, K.A. & Blindheim, J., 2000. Variations in the Atlantic inflow to the Nordic Seas, 1955–1996. *Deep-Sea Research Part I-Oceanographic Research Papers*, **47**, 1035–1057.

Orvik, K.A., Skagseth, O. & Mork, M., 2001. Atlantic inflow to the Nordic Seas: current structure and volume fluxes from moored current meters, VM-ADCP and SeaSoar- CTD observations, 1995–1999. *Deep-Sea Research Part I-Oceanographic Research Papers*, **48**, 937–957.

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

Purcell, J.E., 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. *Marine Ecology Progress Series*, **246**, 137–152.

Purcell, J.E., 2005. Climate effects on jellyfish and ctenophore blooms: a review. *Journal of the Marine Biological Association of the United Kingdom*, **85**, 461–476.

Purcell, J.E. & Arai, M.N., 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia*, **451**, 27–44.

Purcell, J.E. & Decker, M.B., 2005. Effects of climate during 1987–2000 on relative predation by ctenophores and scyphomedusae on copepods in Chesapeake Bay. *Limnology and Oceanography*, **50**, 376–387.

Purcell, J.E. & Sturdevant, M.V., 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Marine Ecology Progress Series*, **210**, 67–83.

Purcell, J.E., White, J.R., Nemazie, D.A. & Wright, D.A., 1999. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha. Marine Ecology Progress Series*, **180**, 187–196.

Reid, P.C., Edwards, M., Beaugrand, G., Skogen, M. & Stevens, D., 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fisheries Oceanography*, **12**, 260–269.

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

Russell, F.S., 1970. *The Medusae of the British Isles. II. Pelagic Scyphozoa with a Supplement to the First Volume on Hydromedusae.* London: Cambridge University Press.

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

Tunberg, B.G. & Nelson, W.G., 1998. Do climatic oscillations influence cyclical patterns of soft macrobenthic communities on the Swedish west coast? *Marine Ecology Progress Series*, **170**, 85–94.

Wegner, G., Damm, U. & Purps, M., 2003. Physical influences on the stock dynamics of plaice and sole in the North Sea. *Scientia Marina*, **67**, 219–234.

Xian, W., Kang, B. & Liu, R., 2005. Jellyfish blooms in the Yangtze Estuary. *Science, New York*, **307**, 41.

Submitted 14 September 2004. Accepted 11 February 2005.