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Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation

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Abstract

Pronounced interannual variability in the abundance of medusae of the jellyfish species *Aurelia aurita, Cyanea lamarckii,* and *Cyanea capillata* (Phylum Cnidaria, Class Scyphozoa) in the North Sea was evident in data arising from the International Council for the Exploration of the Seas International 0-group Gadoid Surveys between 1971 and 1986. Possible climatic forcing of jellyfish abundance, via the North Atlantic Oscillation (NAO), was investigated with data on medusae from four areas of the North Sea (east of Scotland, north of Scotland, east of Shetland, and west of northern Denmark). There were significant inverse relationships between medusa abundance and the NAO Index (December–March) in two regions: west of northern Denmark (*A. aurita* $r^2 = 0.70$, $P = 0.003$, $n = 10$; *C. lamarckii* $r^2 = 0.74$, $P = 0.002$, $n = 10$) and east of Scotland (*A. aurita* $r^2 = 0.53$, $P = 0.008$, $n = 12$). Fluctuations in the abundance of *A. aurita* and *C. lamarckii* medusae might be linked to hydroclimatic changes induced through atmospheric effects (as encapsulated in the NAO Index) on wind stress, temperature, and currents. These fundamental hydroclimatic changes alter the timing of spring phytoplankton blooms and zooplankton community composition. Predation by an abundance of medusae on zooplankton and ichthyoplankton could affect the North Sea ecosystem through top-down and bottom-up mechanisms. Because the NAO is presently in a high phase, climatic conditions could be serving to depress the abundance of medusae: a future reversal of the NAO might favor jellyfish and weaken the persistence or recovery of fisheries.

Jellyfish abundance is increasing in numerous marine ecosystems worldwide, perhaps as a consequence of ‘‘regime shifts’’ associated with climatic change, increasing fishing pressure, or both (Goy et al. 1989; Brodeur et al. 1999; Brierley et al. 2001; Mills 2001). Scyphomedusae can consume large numbers of zooplankton (including copepods, Behrends and Schneider 1995; Purcell 2003) that could otherwise be food for fish, and can also consume fish eggs and larvae (Purcell and Arai 2001). Jellyfish are therefore potentially detrimental to fisheries, both as competitors with, and predators of, fish. It has been suggested that environmental variation affects the abundance and distribution of jellyfish medusae over a range of temporal and spatial scales (Goy et al. 1989; Graham et al. 2001). It has also been shown that food availability, light, salinity, and temperature are all important to the strobilation of scyphistomae (i.e., the development of ephyrae by the sessile polyp) and the survival of medusae (Russell 1970; Purcell et al. 1999; Lucas 2001). There is a growing awareness that large-scale climatic variation can lead to changes in zooplankton community composition and abundance, and that this, in turn, can have major consequences for fisheries (Edwards et al. 2002; Reid et al. 2003). With ever-declining world fish stocks (Hutchings 2000; Pauly et al. 2002) and possible concomitant increases in jellyfish (Mills 2001), it is important to understand the role that climatic forcing might play in influencing jellyfish abundance and the mechanisms by which it could contribute to ecosystem variability (Attrill and Power 2002; Brodeur et al. 2002; Parsons and Lalli 2002).

The North Atlantic Oscillation (NAO) is a climatic phenomenon that contributes greatly to variability in the weather system over the North Atlantic, North Sea, and Europe and has been shown to affect both marine and terrestrial ecosystems (Marshall et al. 2001; Ottersen et al. 2001; Beaugrand et al. 2002). The NAO Index (NAOI) is a measure of the difference in pressure between the Icelandic Low and the Azores High (Hurrell 1995). When the NAO is in its ‘‘high’’ phase and the NAOI is positive, the pressure dipole is pronounced and strong westerlies transport warm air to Northern Europe, resulting in warmer-than-average winters and relatively warm water in the North Sea. The ‘‘low’’ phase (negative NAOI) is characterized by a much weaker Azores High and approximately the reverse of the system described above. The NAO is significantly related to sea level pressure, surface winds, wave heights, sea surface temperature, and current influx to the North Sea (Beaugrand 2003) and has the potential to influence profoundly the pelagic environment. Jellyfish are able to respond rapidly to favorable en-

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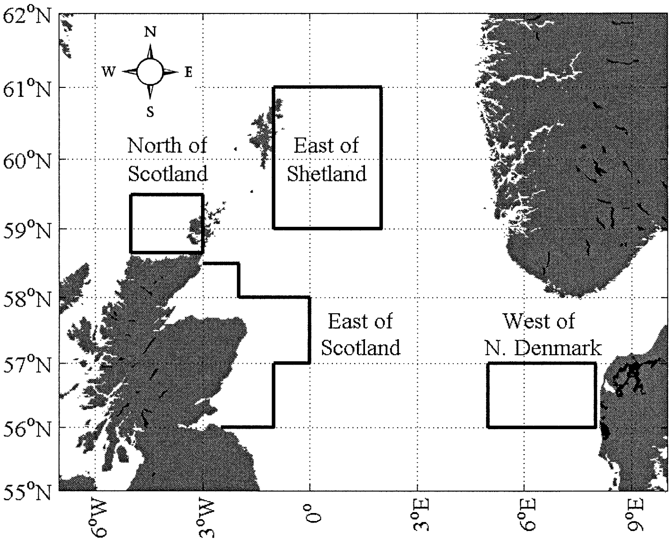

Fig. 1. Map showing the four survey areas in the North Sea.

vironmental conditions, and blooms in their abundance could provide a biological indication of interannual variation in hydroclimatic conditions. Thus, it is expected that, if influential, NAO-related effects on the ecosystem could rapidly become evident in jellyfish populations.

Using data on the abundance of medusae of *Aurelia aurita, Cyanea lamarckii,* and *Cyanea capillata* from the North Sea, we explore here the possibility that jellyfish populations respond to climatic variation as quantified by the NAOI.

Methods

Jellyfish sampling—Medusa abundance data were collected over 15 yr (1971–1986, excluding 1984) during the routine summer International Council for the Exploration of the Sea (ICES) International 0-group Gadoid Surveys of the North Sea (Fig. 1) (Hay et al. 1990). Surveys, of which jellyfish were bycatch, were conducted with the International Young Gadoid Pelagic Trawl (IYGPT). Every year, trawls were conducted during June and July, and for the years 1971 and 1972, hauls were also made in August. The maximum number of trawls made in any one year was 215 (in 1979) and the minimum was 43 (in both 1985 and 1986). From 2,030 IYGPT trawls throughout the North Sea in this period, more than 430,000 medusae were caught, identified, and measured. Three species of jellyfish were particularly conspicuous: *A. aurita, C. lamarckii,* and *C. capillata.*

The IYGPT had mesh sizes of 100 mm in wings, bosom, and belly, tapering through intermediate mesh size to 10-mm knotless meshing in the extension piece and codend. The mouth opening of the net was ~14 m^2. When fished at a maximum speed of 2.5 knots for 1 h, about 65,000 m^3 of water was filtered, assuming 100% filtration efficiency (Hay et al. 1990). During the gadoid surveys, the trawl was fished for 1 h in a standard depth profile. For the first third (0–20 min) of the trawl duration, the net was fished close to the seabed. The net was then hauled to midwater, or to thermocline depth where this was known, and fished for a further 20 min. During the third period of the trawl, the net was fished close to the surface (5–10 m). In depths >150 m, 125 m was taken as the bottom depth; in depths <30 m, only the bottom and surface were fished (for 30 min each, Hay et al. 1990).

The catches of medusae probably provided conservative estimates of actual abundance because of the variable mesh sizes and the variable sizes of medusae. The stepped vertical haul profile could also have led to bias in estimations (Hay et al. 1990). Nevertheless, the same method was used each year, and a broad range of medusa diameters (1–47 cm) were caught in the samples. The sampling efficiency was internally consistent, and catch data are therefore directly comparable between years.

Hay et al. (1990) chose to report median medusa catch values to provide an index of jellyfish abundance (the distributions of catches were nonnormal, rendering the mean unacceptable as a maximum likelihood estimator). The heavily skewed distributions were attributable to the patchiness and sudden blooms of jellyfish populations, resulting in a high proportion of nil catches and a few extremely high catches.

Hay et al. (1990) identified four areas of the North Sea (Fig. 1) that were representative of the major areas of jellyfish abundance. However, the regions were not sampled uniformly, but as follows: east of Shetland (ESh) 1971–1986 excluding 1984 (14 yr), north of Scotland (NoS) 1974 and 1976–1986 excluding 1984 (11 yr), east of Scotland (EoS) 1971–1983 (13 yr), and west of northern Denmark (WND) 1972 and 1975–1983 (10 yr).

Analysis of the interannual variation in abundance of jellyfish with the NAOI—To test for links between medusa abundance and the NAO, we investigated data for each species in each area separately, except ESh, where too few *A. aurita* and *C. lamarckii* medusae were caught to enable robust statistical analysis. A normalized index of the NAO was obtained from the National Center for Atmospheric Research (Climate and Global Dynamics Division [U.S.A.], http://www.cgd.ucar.edu/~jhurrell/). The winter (December–March) NAOI of the normalized sea level pressure (SLP) difference between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland coincides with the biologically important period of ephyra production and development in the North Sea (Russell 1970). The SLP anomalies at each station were normalized by division of each mean pressure for the period December–March by the long-term (1865–1984) mean standard deviation. Normalization was used to avoid domination of the series by the greater variability of the Stykkisholmur/Reykjavik station (Hurrell et al. 2003). To compare temporal changes in abundance of medusae between the regions, the species data were scaled (by subtracting the mean abundance from the yearly median abundance and then dividing by the maximum value of the resulting time series) and plotted against the inverted NAOI (scaled and inverted by dividing by the minimum value of the time series). For *A. aurita* and *C. lamarckii* from WND and *A. aurita* from EoS, an association was apparent (Fig. 2).

All medusa abundance data were natural logarithm transformed to normalize the distributions prior to further statis-

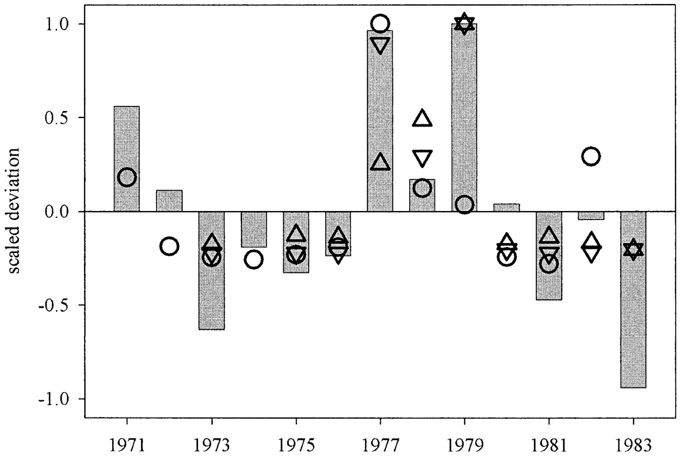

Fig. 2. Normalized NAO (December–March) Index (bars) and jellyfish abundance in the North Sea (*Aurelia aurita*: down triangles, west of northern Denmark; circles, east of Scotland; *Cyanea lamarckii*: up triangles, west of northern Denmark). The NAO Index data were scaled and inverted for ease of visual interpretation by dividing by the minimum value of the time series. The species abundance data were normalized by subtracting the mean and dividing by the maximum value of the remaining points for each series.

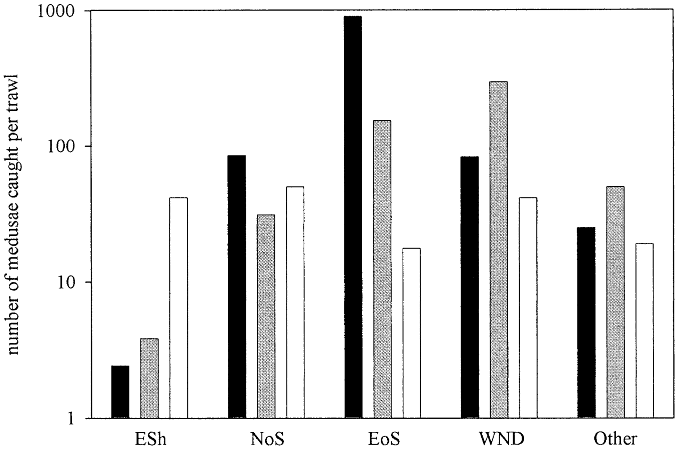

Fig. 3. Distribution of jellyfish catch per trawl by region. Black bars, *Aurelia aurita*; grey bars, *Cyanea lamarckii*; white bars, *Cyanea capillata.*

tical analyses. Species ln(median abundance) and the NAOI were also assessed for linear temporal trends prior to use in statistical analysis by taking a least squares fit of the data (Y_t) against an index of time (T) as in Eq. 1,

$$Y_t = \alpha_0 + \alpha_1 \cdot T \tag{1}$$

where T is measured in years. Temporal trends were judged at the 0.05 level of significance with a standard Student's t-test of the estimated slope parameter. No evidence of temporal trends was found (all $r^2 < 0.10$, $P > 0.30$).

Linear regressions of natural logarithm–transformed abundance data against the NAOI were made for each species in each area (R software v1.4.1) to compute models of the form in Eq. 2.

$$A_t = \beta_0 + \beta_1 \cdot N_t + e_t \tag{2}$$

A_t is the natural logarithm of the medusa abundance value in year t, N_t is the value of the NAOI in year t, e_t is an error term with unit variance and zero mean, and β_0 and β_1 are the intercept and slope parameters, respectively, estimated by linear regression. Similarly, linear regressions were made (Eq. 2) for interspecies and interregion correlations. For interspecies regressions, A_t and N_t represented abundances within the same region of differing species of medusae. For correlations between regions, A_t and N_t represent abundances of the same species of medusae in differing regions. Parameters were assessed at the 0.05 level of significance by a Student's t-test. The model assumptions (linearity, homogeneity of variance, normality, and independence of residuals) were tested following procedures outlined in Krzanowski (1998). In addition, the Shapiro–Wilk W statistic (Dunn and Clark 1974) was used to test residuals for normality and was assessed at the 0.05 level of significance. Outliers were distinguished with the mean shift outlier model: the largest absolute studentized residual was tested with the t distribution and the Bonferroni correction at the 0.10 level of significance (Fox 1997). The Durbin–Watson DW statistic (Draper and Smith 1981) was used to assess residuals for first-order autocorrelation, and the Breusch–Godfrey test (Johnston 1984) was used to assess higher order serial correlation. The significance level for each test was chosen to minimize corresponding Type II error (Krzanowski 1998).

Results

Eighty-five percent of all *A. aurita* and 32% of *C. lamarckii* medusae were caught in the region EoS. However, per trawl, *C. lamarckii* was most abundant (300 medusae per trawl) WND (Fig 3), and *C. capillata* was most abundant NoS (50 medusae per trawl). None of the species were abundant ESh (all species <50 medusae per trawl).

The ln(median abundance) (medusae caught per hour, *see* Hay et al. 1990) of *A. aurita* significantly correlated with that of *C. lamarckii* in all regions analyzed (WND, $r^2 = 0.58$, $P = 0.011$, $n = 10$; EoS, $r^2 = 0.34$, $P = 0.037$, $n = 13$; NoS, $r^2 = 0.44$, $P = 0.026$, $n = 11$). One significant correlation was found between the regions EoS and WND for *A. aurita* ln(median abundances) ($r^2 = 0.44$, $P = 0.048$, $n = 9$), in which one outlier was identified and removed (year 1983, Bonferroni-corrected $P = 0.011$, $n = 10$). When the outlier year was included, the correlation between abundances failed the homogeneity of variance test. No other significant correlations ($P < 0.10$) between medusa abundances were found.

The ln(median medusa abundance) during June–August in the North Sea was inversely correlated with the preceding December–March NAOI for both *A. aurita* (WND, $r^2 = 0.70$, $P = 0.003$, $n = 10$, Fig. 4a; EoS, $r^2 = 0.53$, $P = 0.008$, $n = 12$, Fig. 4b) and *C. lamarckii* species (WND, $r^2 = 0.74$, $P = 0.002$, $n = 10$, Fig. 4c). For *A. aurita* catches in the region EoS only, the abundance value for the year 1983 was identified again as an outlier and removed (Bonferroni-corrected $P = 0.070$, $n = 13$). When the outlier was included, the correlation of *A. aurita* abundance against the NAOI was not significant ($r^2 = 0.13$, $P = 0.22$, $n = 13$).

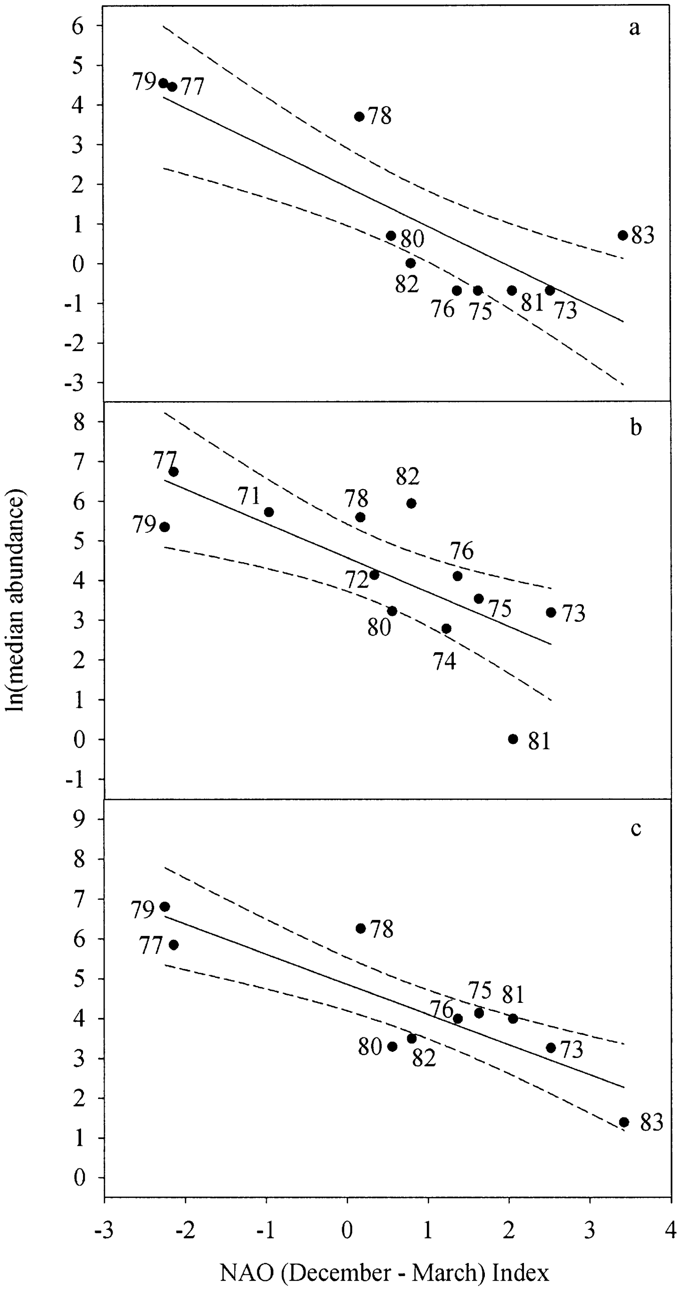

Fig. 4. Linear regressions of jellyfish abundance against the NAO (December–March) Index. Solid line, model fit; dashed lines, 95% confidence interval. (a) *Aurelia aurita,* west of northern Denmark, $r^2 = 0.70$, $P = 0.003$, $n = 10$, $y = 1.9 - 1.0x$. (b) *A. aurita,* east of Scotland, $r^2 = 0.53$, $P = 0.008$, $n = 12$, $y = 3.0 - 0.6x$. (c) *Cyanea lamarckii,* west of northern Denmark, $r^2 = 0.74$, $P = 0.002$, $n = 10$, $y = 5.0 - 1.0x$.

The assumptions of linearity, homogeneity of variance, normality, and independence of residuals were upheld by all significant regressions. No significant ($P < 0.05$) linear temporal correlations were found in the abundance of medusae or the NAOI data. No autocorrelation or higher order serial correlations were present in the data.

No correlations with the NAOI were found for *C. capillata* as an individual species. Significant ($P < 0.05$) relationships between medusa abundance and the NAOI were found for the summation of each species' median catch by each region and for all regions combined, as well as sums of median catches of pairwise combinations of species by region and for all regions combined. However, all r^2 values for these summations were low relative to those reported for individual species by region, indicating that these combinations merely decreased the proportion of population variability that could be explained by the regression.

Discussion

For the first time, we have shown that interannual variation in the abundance of medusae in the North Sea could be driven by changes in the climate as quantified by the NAO winter index. A jellyfish–climate interaction has previously been proposed for the Bering Sea ecosystem, but a statistically significant link has not been demonstrated (Brodeur et al. 1999).

Numerous NAO-related factors could influence fish and jellyfish abundance in the North Sea, where the NAOI is positively correlated with the western component of wind stress, sea surface temperature, and changes in the influx of Atlantic and Norwegian water (Beaugrand 2003; Reid et al. 2003). NAO-related effects of the hydroclimatic environment are evident in the timing and abundance of the North Sea spring phytoplankton bloom and changes in the zooplankton community structure (Edwards et al. 2002; Reid et al. 2003). The rapid growth of medusae and short life span (usually 8–10 months) suggest that jellyfish would show a same-year response to climatic changes; thus, no lag is to be expected in regressions of abundance against the NAOI. Our data are insufficient to elucidate the exact mechanisms by which climate affects jellyfish populations, but we present two possible scenarios within the framework of a conceptual model (Fig. 5a,b). The NAO-related mechanisms might act directly between the climate and jellyfish by altering advective dispersal/concentration of ephyrae (juvenile medusoids) aggregations or via changes in temperature, salinity, light, and current strength to improve conditions for ephyra release and growth (Purcell et al. 1999; Graham 2001; Lucas 2001). Alternatively, the mechanisms linking the climatic changes to interannual jellyfish population variation could be indirect, resulting in improved availability of prey to the growing jellyfish, either by altering the timing of the spring bloom to synchronize with the period of rapid ephyral growth or by increasing the abundance of zooplankton or ichthyoplankton prey to juvenile medusae (Båmstedt et al. 2001; Edwards et al. 2002; Platt et al. 2003). Therefore, there could be an effect of jellyfish on fisheries either through top-down (medusae prey on fish eggs and larvae) or bottom-up processes (medusae reduce zooplankton abundance, including copepods, thus limiting fish populations) (Schneider and Behrends 1998; Purcell and Arai 2001).

Although we found strong correlation for *A. aurita* and *C. lamarckii* abundances with the NAOI, we found none for *C. capillata.* A number of factors might contribute to this absence of association. In contrast to the other species, overwintering *C. capillata* medusae were found to contribute sig-

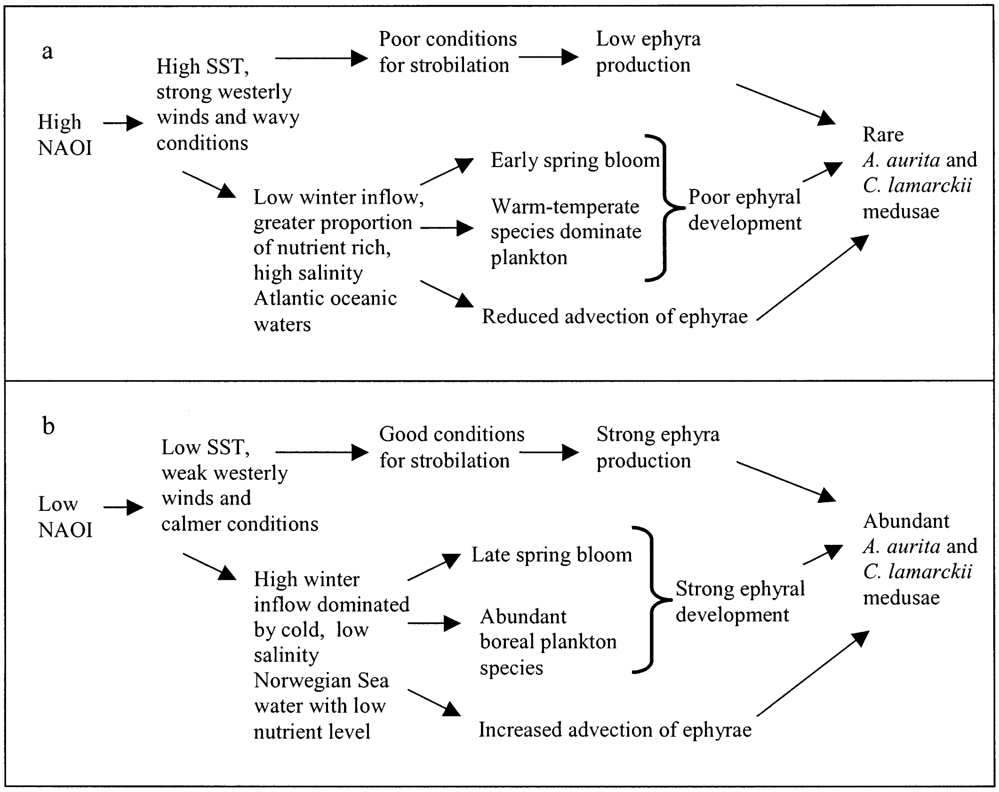

Fig. 5. A conceptual model of the possible associations between the NAO—(a) high/+ve index, (b) low/−ve index—and the North Sea jellyfish *Aurelia aurita* and *Cyanea lamarckii.*

nificantly to the summer biomass (Hay et al. 1990). Therefore, *C. capillata* might exhibit multiple generations (although it is unlikely that this would extend to more than two generations), and any single-year effects of changes in the NAO on the population might be spread and confounded over a number of years. Hay et al. (1990) also noted that variable numbers of *C. capillata* and *A. aurita* each year had drifted westward from Norwegian coastal waters into the deep offshore waters outside the survey area. *C. capillata* has a more northerly dispersed spatial distribution relative to the other species, and this species was found to be most abundant in the region NoS. Here, the NAO appears to be less influential on sea surface temperature (SST) relative to the other regions, possibly because of variation in salinity through changes in the relative inflow of Atlantic and Norwegian waters. Becker and Pauly (1996) found that the NAOI was significantly spatially correlated with SST anomalies in the North Sea, with high correlation in the central North Sea and in the area covering the region WND, where correlations with medusa abundance were found to be most explanatory. So, the more complex hydrographical conditions found in the northern regions (ESh and NoS) might obscure any NAO-related effects on the pelagic ecosystem.

Strobilation of scyphistomae in *Aurelia* and *Cyanea* spp. is triggered environmentally following a change in sea temperature (Russell 1970; Brewer and Feingold 1991; Miyake et al. 2002). Therefore, SST anomalies could affect the strobilation process and might partly explain the link between medusa abundance and the NAOI. Lucas (2001) suggested that the timing of initiation and the duration of the strobilation process might be dependent on both the winter minimum temperature and on food availability. Omori et al. (1995) proposed that environmental conditions during the polyp stage of *A. aurita* could govern mass occurrences of the medusae. In the North Sea, jellyfish ephyrae are produced and released during the winter and early spring months from sessile scyphistomae (Russell 1970) when the NAO has greatest influence on the North Sea. The NAO therefore might play an important role in mediating the environmental conditions that affect scyphistomae strobilation.

Planque and Taylor (1998) report on modeling work that shows significant ($P < 0.01$) correlations between inflow of Atlantic water to the North Sea during the winter and the NAOI. However, it would appear that the study might have integrated both Norwegian and Atlantic influx. Recent work by Reid et al. (2003) suggests that a composite relationship might exist between the NAOI and inflow: these authors found that during the first 3 months of the year, the NAOI was positively correlated with inflow for an upper layer of water (0–150 m), representing Atlantic influx, and negatively correlated with deeper water (150–500 m) that they suggested derives from the Norwegian Sea via the Norwegian Trench. If we consider Planque and Taylor's (1998) study in this light, it appears that the negative correlations they found between inflow of water (east of Shetland and west of Norway) and the NAOI might represent dominance by Norwegian deep water, whereas the positive correlation between inflow through the passage between Orkney and Shetland might represent dominance by Atlantic water.

Even if the relationship between the NAOI and the abundance of medusae shown in the southern regions were to hold in the regions ESh and NoS, the effect could be masked by changes in advection. Assuming that ephyrae are present ESh and NoS, advection from these regions might result in a more southerly distribution of medusae during the summer and thus more concentrated aggregations EoS and WND. An extreme example of this process might explain the outlier year (1983) detected in the *A. aurita* data EoS. During 1983, Atlantic herring moved from their northern spawning grounds to Aberdeen Bank, a ground that had not been used for 16 years, and this reappearance has been attributed to an unusual late summer inflow of Atlantic water to the North Sea (Corten 1999). Advection to/from the Skagerrak, where medusae are often abundant, might also explain some of the variation in the abundance of medusae WND. However, the high abundance of medusae recorded WND in 1977, 1978, and 1979 coincides with an unusual negative salinity anomaly that was measured between 1977 and 1981 in the entrance of the Skagerrak and attributed, because of the presence of arctic-boreal species, to advection from the Norwegian Trench rather than from the Skagerrak (Edwards et al. 2002).

Reid et al. (2003) describe a ‘‘cold biological event’’ between 1978 and 1982 linked to decreased inflows of warm Atlantic water (evident in the reduced netflow of an upper-water layer [$<$150 m]) and increased inflows of colder, deeper (150–500 m) Norwegian water carrying boreal indicator plankton species (e.g., *Calanus hyperboreus, Euchaeta norvegica,* and *Metridia longa*) into the North Sea. This cold biological event coincided with reduced copepod diversity in the North Sea that was significantly correlated with the NAOI (Beaugrand 2003). In 1979, the year of highest recorded *A. aurita* and *C. lamarckii* medusa abundance WND, *C. hyperboreus* was recorded as far south as the entrance to the Skagerrak, and the cold-water dinoflagellate *Ceratium longipes* was found to be five standard deviations above its long-term mean abundance, while *Ceratium macroceros* experienced a population crash, and other resident phytoplankton species were found in unusually low abundance in the North Sea (Edwards et al. 2002). Overall, the cold biological period coincided with low abundance of dinoflagellates, diatoms, decapod larvae, and copepods, with substantial declines in herring and western mackerel stocks, while arctic-boreal plankton species and both *A. aurita* and *C. lamarckii* medusae were particularly abundant.

The effects on the North Sea ecosystem of pollution, overfishing, and climatic change and their subsequent effects on jellyfish are difficult to evaluate separately because these factors can interact to alter the marine environment. Arai (2001) demonstrated that scyphomedusae might benefit from eutrophication and suggested that the high abundance of *C. lamarckii* WND might be linked to eutrophication there. The North Sea ecosystem might also have been modified through ‘‘fishing down the food web’’ from long-lived, high–trophic level, piscivorous bottom fish toward short-lived, low–trophic level invertebrates and planktivorous pelagic fish (Hutchings 2000; Pauly et al. 2002).

Populations of *A. aurita* and *C. lamarckii* appear to be indicators of ecosystem variability, and interannual population fluctuations in abundance or distribution might be driven through climatic changes. Because jellyfish have the potential to play an important role in ecosystem control or to proliferate following high fishing effort (Purcell and Arai 2001), further study to elucidate mechanisms through which jellyfish respond to climatic changes and the subsequent effects on fisheries is essential.

The inverse relationships found between the winter NAOI and the median abundance of medusae could imply that cooler, calmer conditions and possible changes in current influx (including a greater inflow of Norwegian water relative to Atlantic water) to the North Sea during the winter–spring period of ephyra release and growth lead to greater abundances of *A. aurita* and *C. lamarckii* medusae in the regions EoS and WND in the summer months.

The present NAO high might exert a negative influence on *A. aurita* and *C. lamarckii* medusae, suppressing abundance. We speculate that a future reversal of the NAO phase could release the environmental inhibition on these jellyfish. North Sea fish stocks are presently in a perilous state. A boom in medusae could exacerbate the situation and might hinder the recovery of fish stocks, even following the cessation of fishing.

References

ARAI, M. N. 2001. Pelagic coelenterates and eutrophication: A review. Hydrobiologia **451:** 69–87.

ATTRILL, M. J., AND M. POWER. 2002. Climatic influence on a marine fish assemblage. Nature **417**(6886): 275–278.

BÅMSTEDT, U., B. WILD, AND M. B. MARTINUSSEN. 2001. Significance of food type for growth of ephyrae *Aurelia aurita* (Scyphozoa). Mar. Biol. **139:** 641–650.

BEAUGRAND, G. 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. Fish Oceanogr. **12:** 270–283.

———, P. C. REID, F. IBANEZ, A. J. LINDLEY, AND M. EDWARDS. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science **296:** 1692–1694.

BECKER, G. A., AND M. PAULY. 1996. Sea surface temperature changes in the North Sea and their causes. ICES J. Mar. Sci. **53:** 887–898.

BEHRENDS, G., AND G. SCHNEIDER. 1995. Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel-bight (Western Baltic-Sea). Mar. Ecol. Prog. Ser. **127:** 39–45.

BREWER, R. H., AND J. S. FEINGOLD. 1991. The effect of temperature on the benthic stages of *Cyanea* (Cnidaria, Scyphozoa), and their seasonal distribution in the Niantic River estuary, Connecticut. J. Exp. Mar. Biol. Ecol. **152:** 49–60.

BRIERLEY, A. S., B. E. AXELSEN, E. BUECHER, C. A. J. SPARKS, H. BOYER, AND M. J. GIBBONS. 2001. Acoustic observations of jellyfish in the Namibian Benguela. Mar. Ecol. Prog. Ser. **210:** 55–66.

BRODEUR, R. D., C. E. MILLS, J. E. OVERLAND, G. E. WALTERS, AND J. D. SCHUMACHER. 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fish Oceanogr. **8:** 296–306.

———, H. SUGISAKI, AND G. L. HUNT. 2002. Increases in jellyfish biomass in the Bering Sea: Implications for the ecosystem. Mar. Ecol. Prog. Ser. **233:** 89–103.

CORTEN, A. 1999. The reappearance of spawning Atlantic herring (*Clupea herengus*) on Aberdeen Bank (North Sea) in 1983 and its relationship to environmental conditions. Can. J. Fish. Aquat. Sci. **56:** 2051–2061.

DRAPER, N. R., AND H. SMITH. 1981. Applied regression analysis, 2nd ed. John Wiley and Sons.

DUNN, O. J., AND V. A. CLARK. 1974. Applied statistics: Analysis of variance and regression. John Wiley and Sons.

EDWARDS, M., G. BEAUGRAND, P. C. REID, A. A. ROWDEN, AND M. B. JONES. 2002. Ocean climate anomalies and the ecology of the North Sea. Mar. Ecol. Prog. Ser. **239:** 1–10.

FOX, J. 1997. Applied regression, linear models, and related methods. Sage.

GOY, J., P. MORAND, AND M. ETIENNE. 1989. Long-term fluctuations of *Pelagia noctiluca* (Cnidaria, Scyphomedusa) in the western Mediterranean-Sea—prediction by climatic variables. Deep-Sea Res. Oceanogr., A **36:** 269–279.

GRAHAM, W. M. 2001. Numerical increases and distributional shifts of *Chrysaora quinquecirrha* (Desor) and *Aurelia aurita* (Linne) (Cnidaria: Scyphozoa) in the northern Gulf of Mexico. Hydrobiologia **451:** 97–111.

———, F. PAGÉS, AND W. M. HAMNER. 2001. A physical context for gelatinous zooplankton aggregations: A review. Hydrobiologia **451:** 199–212.

HAY, S. J., J. R. G. HISLOP, AND A. M. SHANKS. 1990. North-Sea Scyphomedusae—summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Neth. J. Sea Res. **25:** 113–130.

HURRELL, J. W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. Science **269:** 676–679.

———, Y. KUSHNIR, G. OTTERSEN, AND M. VISBECK. 2003. An overview of the North Atlantic Oscillation. p. 1–35. *In* J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck [eds.], The North Atlantic Oscillation: Climatic Significance and Environmental Impact. Geophysical Monograph 134. American Geophysical Union.

HUTCHINGS, J. A. 2000. Collapse and recovery of marine fishes. Nature **406**(6798): 882–885.

JOHNSTON, J. 1984. Econometric methods, 3rd ed. McGraw Hill.

KRZANOWSKI, W. J. 1998. An introduction to statistical modelling. Arnold.

LUCAS, C. H. 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. Hydrobiologia **451:** 229–246.

MARSHALL, J., AND OTHERS. 2001. North Atlantic climate variability: Phenomena, impacts and mechanisms. Int. J. Climatol. **21:** 1863–1898.

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

MIYAKE, H., M. TERAZAKI, AND Y. KAKINUMA. 2002. On the polyps of the common jellyfish *Aurelia aurita* in Kagoshima Bay. J. Oceanogr. **58:** 451–459.

OMORI, M., H. ISHII, AND A. FUJINAGA. 1995. Life-history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo-Bay. ICES J. Mar. Sci. **52:** 597–603.

OTTERSEN, G., B. PLANQUE, A. BELGRANO, E. POST, P. C. REID, AND N. C. STENSETH. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia **128:** 1–14.

PARSONS, T. R., AND C. M. LALLI. 2002. Jellyfish population explosions: Revisiting a hypothesis of possible causes. La Mer **40:** 111–121.

PAULY, D., AND OTHERS. 2002. Towards sustainability in world fisheries. Nature **418**(6898): 689–695.

PLANQUE, B., AND A. H. TAYLOR. 1998. Long-term changes in zooplankton and the climate of the North Atlantic. ICES J. Mar. Sci. **55:** 644–654.

PLATT, T., C. FUENTES-YACO, AND K. C. FRANK. 2003. Spring algal bloom and larval fish survival. Nature **423:** 398–399.

PURCELL, J. E. 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata, Cyanea capillata* and *Aequorea aequorea,* in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. **246:** 137–152.

———, AND M. N. ARAI. 2001. Interactions of pelagic cnidarians and ctenophores with fish: A review. Hydrobiologia **451:** 27–44.

———, J. R. WHITE, D. A. NEMAZIE, AND D. A. WRIGHT. 1999. Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha.* Mar. Ecol. Prog. Ser. **180:** 187–196.

REID, P. C., M. EDWARDS, G. BEAUGRAND, M. SKOGEN, AND D. STEVENS. 2003. Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fish Oceanogr. **12:** 260–269.

RUSSELL, F. S. 1970. The medusae of the British Isles. II Pelagic Scyphozoa with a supplement to the first volume on Hydromedusae. Cambridge Univ. Press.

SCHNEIDER, G., AND G. BEHRENDS. 1998. Top-down control in a neritic plankton system by *Aurelia aurita* medusae—a summary. Ophelia **48:** 71–82.

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