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Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea

Abstract—Data obtained since 1958 from the continuous plankton recorder show an increasing occurrence of jellyfish in the central North Sea that is positively related to the North Atlantic Oscillation (NAO) and Atlantic inflow to the northern North Sea. Since 1970, jellyfish frequency has been also significantly negatively correlated with mean annual pH, independent of NAO trends. Jellyfish frequency increased in the mid-1980s, coincident with the reported regime shift in the North Sea and tracking trends in phytoplankton color. As models produced under all climate-change scenarios indicate a move toward a positive NAO, and pH of the oceans is predicted to decrease with rising CO_2, we suggest that jellyfish frequency will increase over the next 100 yr.

Jellyfish medusae are key predators in many of the world's pelagic systems (Mills 1995) and can affect the abundance of zooplankton (Purcell 2003), fish larvae, and eggs (Purcell et al. 1994) and thus recruitment of fish populations (Lynam et al. 2005). When in large numbers, they have been implicated in the disruption of pelagic ecosystems (Mills 2001; Stibor et al. 2004), particularly where blooms have formed. Gelatinous plankton are rarely the preferred prey item of other species (Moline et al. 2004) and so have been considered "trophic dead-ends", yet have become the dominant top predator symptomatic of some overfished systems (Brodeur et al. 2002; Hughes et al. 2005). Any large-scale increase in the occurrence of jellyfish could therefore have major consequences for pelagic ecosystems and fisheries. Recent increases in abundance of native (Mills 1995; Brodeur et al. 2002) and introduced (Mills 1995) species have been reported for a range of systems, although decreases have also been noted (Mills 1995; Boldt 2004).

Climate variability has been suggested as one driver for changes in the abundance and distribution of gelatinous plankton (e.g., Brodeur et al. 1999; Lynam et al. 2004; Purcell 2005). Jellyfish abundance during the 1970s–1980s was negatively correlated with the NAO index (NAOI) (Lynam et al. 2004) in the central North Sea, but positively correlated north of Scotland (Lynam et al. 2005) and in the Thames Estuary (Attrill and Power 2002). Since the mid-1980s, however, the North Sea has undergone a major regime shift (Beaugrand 2004), affecting the abundance, distribution, and production of the pelagic environment (Beaugrand et al. 2003; Reid et al. 2003).

Although some long-term data exist (Purcell 2005), time series have generally been too short to clearly assess the role of climate beyond other environmental factors. We used long-term data (43 yr) collected by the continuous plankton recorder (CPR) to investigate whether climate variability or this regime shift has influenced the frequency of occurrence of jellyfish across the North Sea, covering six standard CPR sectors (Fig. 1a), but focusing on areas of previous study to validate trends (C2). Additionally, we investigated past relations between North Sea pH and jellyfish frequency to test the prediction that future increasing acidity due to higher levels of CO_2 in the atmosphere (Calderia and Wickett 2003) may be detrimental to calcareous, skeleton-forming plankton (Riebesell et al. 2000; Hays et al. 2005) and thus allow proliferation of gelatinous organisms. Finally, we utilized the output from climate models (Osborn 2004) to explore possible future trends (Araújo et al. 2005) in jellyfish frequency.

Methods—Biological and environmental data: Jellyfish data used in this study were collected by the CPR survey. This is an upper-layer plankton-monitoring program that has been undertaken in the North Atlantic and North Sea since 1946. Sampling is carried out by a high-speed plankton recorder that is towed at monthly intervals behind merchant ships (at about 20 km h^{-1}) on regular routes at a standard depth of approximately 6.5 m. Use of such vessels means that the sampling frequency in the North Sea has been consistent over both months and years. One CPR sample corresponds to about 3 m^3 of seawater filtered (Warner and Hays 1994). Jellyfish are only recorded in each CPR sample if nematocysts are present in standard phytoplankton or traverse zooplankton searches, indicating at least one medusa has been sampled; it is impossible to enumerate abundance from these samples and we make no attempt to present straight abundance data. Instead, jellyfish occurrence is used in this analysis, namely the percent frequency of nematocysts recorded (presence/absence) on CPR samples in respect to the number of CPR samples taken, providing an indication of how widespread jellyfish are across the North Sea at any one time. Nematocysts can indicate the presence of several pelagic cnidarian groups, in particular scyphomedusae, hydromedusae, and siphonophores. During CPR analysis, siphonophores are separately enumerated, leaving unidentified nematocysts as a potential mix of scyphomedusae and hydromedusae; although separation is possible from nematocyst analysis, this has not been routinely completed. Plankton tows in the coastal west-central North Sea (Nicholas and Frid 1999) that have enumerated Cnidaria demonstrated both groups to be present, but with clear temporal separation. Hydromedusae (mainly *Obelia*) peaked in July/August, with scyphomedusae densities highest in October–December (mainly *Aglantha digitale*). Nematocyst occurrence in CPR samples has predominately peaked late in the year (Fig. 1), and samples are generally taken further

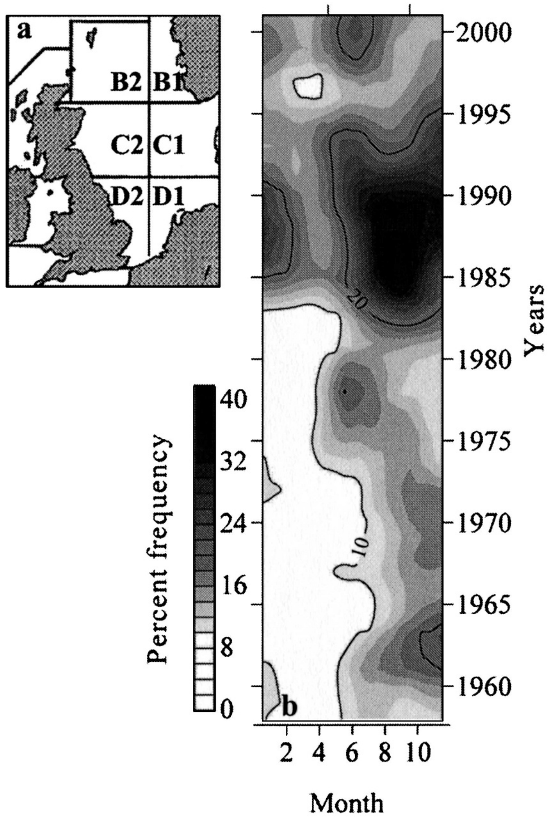

Fig. 1. (a) Diagram of North Sea indicating standard CPR areas sampled in this study. (b) Trends in jellyfish frequency (% occurrence) since 1958: Monthly averages for whole North Sea region (Gaussian smoother applied).

offshore than Nicholas and Frid (1999), in open water, where scyphomedusae dominate (Williams and Conway 1981). For the purpose of this study, we therefore define "jellyfish" as both scyphomedusae and hydromedusae, although available evidence suggests the nematocysts in CPR samples are most likely to be from scyphozoans.

All jellyfish data from the six North Sea CPR regions (Northern B1, B2; Central C1, C2; Southern D1, D2; Fig. 1a) for the 1958–2000 period were extracted from the database. For analysis, the data were then standardized, setting the mean value at zero and 95% of the values occurring within 2 SD above or below the mean. For each region in each year, annual mean phytoplankton color index (PCI) was extracted from the CPR database. This is a visual index of chlorophyll based on the intensity of the green color across the CPR filter and assigned numerical values in four categories. PCI has been demonstrated statistically to reflect primary production in the sea (Reid et al. 1998).

Data for four major environmental variables were also obtained to match the jellyfish data series: NAOI (preceding winter December–March), mean annual sea surface temperature (SST, from the Hadley Centre, UK Met Office [HadISST Version 1.1]), and annual Atlantic inflow for each of six standard CPR North Sea regions. As there are no time series of measured inflow over the timescale of the present study, we have used the flux of Atlantic waters entering the North Sea between the Orkney Islands and Utsira from the NORWECOM three-dimensional hydrodynamic model (influx volume of Atlantic water in Sverdrup) (Iversen et al. 2002). Mean average pH for the central North Sea was calculated using available data from ICES public databases (acceptable and available data with adequate replication in 20 yr between 1971 and 1995, but covering the major fluctuations in jellyfish frequency, total $n = 8{,}879$).

Data analysis: Regression analysis was undertaken between mean annual jellyfish frequency within each North Sea region, and for the sea as a whole, and SST (for the respective region), NAOI, and Atlantic inflow, with α set at 0.05. An additional analysis was completed for the west-central North Sea (C2) between jellyfish frequency and mean pH; relations between pH and the other environmental parameters were also investigated. Any outliers were identified statistically using Grubb's test and removed (one point only, jellyfish frequency for 1987 in C1 and C2 regions) and probability levels adjusted for multiple tests using the Bonferroni correction. For significant relations, residuals were checked for statistical adequacy: normality (Kolgorov–Smirnoff test), and homoscedasticity (scrutinizing plots of standardized residuals). All significant analyses conformed to these regression assumptions. As a temporal trend is apparent in most data sets, and to account for any autocorrelation in the data, detrended analyses were also undertaken to test the robustness of significant relationships by correlating residuals from variable-year regressions (e.g., residuals from NAOI-year vs. residuals from jellyfish-year). To explore potential trends in jellyfish frequency in the future, data were extracted from seven models produced to explore the behavior of the NAOI under a range of climate change scenarios: CSIRO MK2, CGCM1, CCSR/NIES, ECHAM4/OPYC, NCAR PCM, HadCM3, HadCM2 (Osborn 2004). Predicted values for the NAOI until 2100 were then entered into regression models for jellyfish-NAOI relation; the mean trend from these models was also calculated, as recommended for increasing the accuracy of climate–biodiversity predictions (Araújo et al. 2005).

Results—Between 1958 and the mid-1980s, jellyfish frequency varied little beyond seasonal patterns (Fig. 1b). Large increases in frequency during the latter half of each year were apparent post-1984, however, remaining particularly high for the next decade. Although weak significant associations were apparent between jellyfish frequency and time for the central North Sea (C1: $r^2 = 0.123$, $p = 0.019$; C2: $r^2 = 0.282$, $p < 0.001$), frequency was better explained by positive relations with the NAOI (Fig. 2a) and Atlantic inflow index (Fig. 2b) for both central sectors (NAOI: C1, $r^2 = 0.169$; C2, $r^2 = 0.406$. AII: C1, $r^2 = 0.251$; C2, $r^2 = 0.505$. All $p \leq 0.007$). All NAOI relations, and that for C2 inflow, remained significant after detrending. The previous reported negative relation between NAOI and jellyfish abundance for C2 sector (Lynam et al. 2004) appears to be an artifact of that sampling period, the negative trend being nested within the longer-term positive relation (Fig. 2a, open squares are CPR results for these years). For these

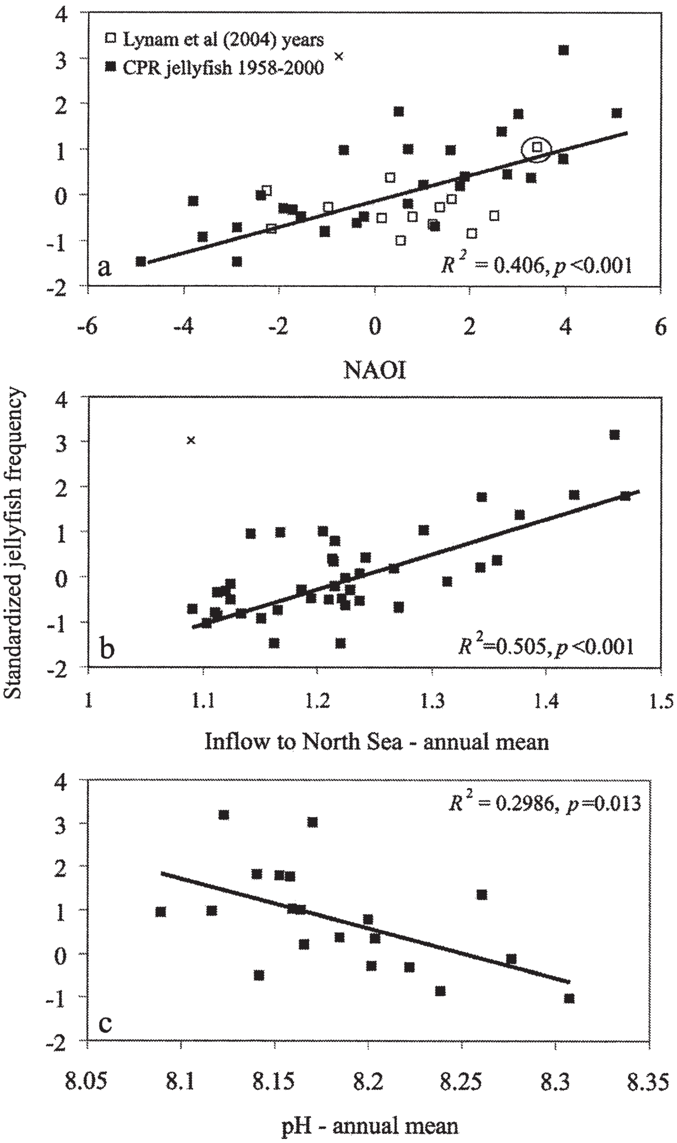

Fig. 2. Relations between standardized jellyfish frequency (1958–2000) and (a) NAOI, (b) Atlantic inflow (Sverdrup), (c) mean annual pH (1971–95) for region C2 (west-central North Sea), together with trend lines and regression statistics. CPR data from years matching those reported by Lynam et al. (2004) displayed as open squares in panel (a), demonstrating their reported negative relation is nested within a longer-term positive trend. Ringed point is outlier from Lynam et al. (2004, 2005) trend (see text). n = 43 (a, b), n = 20 (c); x = outlier identified using Grubb's test and removed.

years, there is a positive rank correlation between our CPR data and the Lynam et al. (2004, 2005) *Aurelia* data series (r = 0.348), strengthened by the removal of one outlier point (1979: r = 0.641, p = 0.025, n = 12). This indicates consistency between the two different sampling programs in terms of assessing jellyfish fluctuations. There were no significant associations between jellyfish abundance and SST, nor robust, consistent relations between jellyfish frequency and any environmental variables for B or D sectors (Table 1), contrary to the findings of previous shorter time series (Lynam et al. 2005). A significant negative relation was apparent between C2 jellyfish abundance and mean annual pH for the years 1971–1994, when noncoastal pH data were available for that central North Sea region (Fig. 2c), remaining significant after detrending. pH was not significantly correlated with NAOI, inflow, SST, salinity, PCI, or time over this period (all $p > 0.05$) . For all sectors except D2, jellyfish frequency was positively correlated with PCI (all r = 0.517−0.867, $p \leq 0.001$, n = 35) that was used to highlight the North Sea regime shift (Beaugrand 2004), indicating a possible link between primary production and jellyfish frequency.

Utilizing our model for the NAOI-jellyfish relation (Fig. 2a) and assuming the pattern over the last 40 yr continues, possible trends in jellyfish frequency were explored using outputs from seven simulation models of NAO behavior under different emission scenarios until 2100 (Osborn 2004). Models predicted a range of increasing frequency of jellyfish in the North Sea (Fig. 3), with the central tendency (which reduces uncertainty in projections [Araújo et al. 2005]) demonstrating a near-linear upward trajectory over the next 100 yr.

Discussion—The relation between the NAO and jellyfish frequency within region C2 is the opposite to previous observations made over a shorter time period (Lynam et al. 2004), demonstrating an increasing rather than decreasing trend. The previous negative trend in the North Sea (which was noted as a global anomaly [Purcell 2005]) is apparent within our longer data set and appears to be an artifact of those particular years that do not encompass the extreme ends of the NAOI range. Additionally, Lynam et al. (2004, 2005) removed one outlier (1983) to produce a significant negative trend. This year had an apparently anomalously high abundance at high NAOI, but can be seen to be situated practically on the trend line of our positive relation (ringed point in Fig. 2a). The positive relation was also apparent in the eastern central North Sea (C1), but no relation existed between jellyfish frequency and environmental variables for either the southern North Sea or the northern part of the region. Previously, the shorter time series had demonstrated a positive association between jellyfish and NAOI north of Scotland (Lynam et al. 2005), but this does not appear to be maintained when the time series is expanded.

Jellyfish frequency, therefore, is influenced by climatic variability across the main central North Sea, but not in northern or southern regions. The close relation between jellyfish and Atlantic inflow provides a mechanism that explains this observed association, the amount of inflow into the North Sea being primarily driven by the climatic oscillation (Reid et al. 2003). Increased inflow results either in favorable conditions for jellyfish, or actively brings more jellyfish into the central North Sea, resulting in the significant link between climate and jellyfish frequency. The second mechanism is more likely, as the maximum abundance of jellyfish occurs in the autumn/winter coincident with maximum Atlantic inflow into the North Sea (Reid et al. 2003). This inflow is not sufficient to influence the southern North Sea, and the region to the North provides more consistent conditions for jellyfish and is

Table 1. Results of bivariate correlation analyses (Pearson's) between mean annual jellyfish frequency in each North Sea sector (e.g., B1 = mean annual frequency for sector B1) and NAOI, Atlantic inflow index, and sea surface temperature (annual mean for each sector). All $n = 42$. One separate analysis on existing ICES data for mean annual pH and C2 jellyfish frequency ($n = 20$). All significant results are in bold; those in italics are not significant after Bonferroni adjustment for multiple tests. For all significant results where a significant temporal trend in the data for the variable pair was apparent (all except pH), detrended analysis was undertaken by correlating the residuals from variable-year regressions.

	Pearson's correlation		Detrended correlation analysis	
Pair of variables	r	*p*	r	*p*
B1 versus NAOI	0.249	0.112		
B1 versus inflow	0.315	***0.042***	0.031	0.844
B1 versus SST	0.083	0.602		
B2 versus NAOI	0.158	0.319		
B2 versus inflow	−0.140	0.375		
B2 versus SST	−0.125	0.431		
C1 versus NAOI	0.412	**0.007**	0.387	**0.010**
C1 versus inflow	0.501	**0.001**	0.267	0.084
C1 versus SST	0.211	0.180		
C2 versus NAOI	0.637	**<0.001**	0.796	**<0.001**
C2 versus inflow	0.711	**<0.001**	0.741	**<0.001**
C2 versus SST	0.213	0.180		
C2 versus pH	−0.546	**0.013**	−0.460	**0.042**
D1 versus NAOI	0.016	0.920		
D1 versus inflow	0.321	***0.038***	0.284	0.069
D1 versus SST	−0.018	0.911		
D2 versus NAOI	0.226	0.150		
D2 versus inflow	0.283	0.069		
D2 versus SST	0.160	0.311		
Whole Sea versus NAOI	0.330	***0.033***	0.360	**0.019**
Whole sea versus inflow	0.066	0.680		
Whole sea versus SST	−0.061	0.703		

above the main area influenced by changes in inflow. For this mechanism, a link with NAO would therefore not be expected in these two areas, as observed.

The first large increases in jellyfish frequency coincided with the reported 1980s regime shift in the North Sea that has resulted in different phytoplankton and copepod assemblages (Beaugrand 2004). The response of jellyfish at this time has not been considered previously, but their increasing frequency across the North Sea correlates positively with changes in phytoplankton color (and thus production) that also increased significantly in the 1980s (Reid et al. 1998). Changes to the zooplankton assemblage during this regime shift have been suggested as a bottom-up control of North Sea cod populations. We have no direct evidence to suggest that jellyfish predation may be directly affecting cod stocks, but such a top-down control by jellyfish has been suggested for other fisheries (Purcell et al. 1994; Lynam et al. 2005), and the coincident increase in jellyfish (or the more widespread existence of jellyfish throughout the year, removing any previous seasonal mismatch) should be considered as another possible factor that has affected cod (and other fish) recruitment. Alternatively, increasing jellyfish frequency may be as an opportunistic response to the reduction in other commercially caught predators (Hughes et al. 2005). The causality requires further investigation, but our results demonstrate that jellyfish clearly increased in frequency coincident with the regime shift and therefore are likely to have been influencing the ecosystem since this time.

The association between pH and jellyfish occurrence is the first time (that we are aware of) that increased occurrence of gelatinous organisms with reducing pH has been demonstrated. From available data, annual mean pH varied by 0.2 over the time period studied (though with no temporal trend), predicted decreases in oceanic pH with rising CO_2 over the next century being up to 0.3 units (Hays et al. 2005). Such a decrease has been suggested to severely affect calcifying plankton and other skeleton-forming organisms (Riebesell et al. 2000; Hays et al. 2005), so would potentially favor noncalcifying organisms such as jellyfish. The relation we demonstrate here over the central North Sea supports such a prediction, with increased jellyfish occurrence in years where the water was more acidic. The mechanism for pH changes in these data is unclear, as pH over this 20-yr data set was not correlated with any other variable beyond jellyfish occurrence, including potential drivers such as salinity, temperature, and PCI. pH may therefore be acting as a secondary axis to NAO/inflow as an explanatory variable for increases in jellyfish occurrence, although this is more likely to be indirect through other changes in the pelagic community.

The significant positive relation between jellyfish and NAO over the last 40 yr allowed exploratory models of jellyfish frequency trends to be constructed, all emission-scenario model outputs suggesting that the frequency of occurrence of jellyfish will most likely increase over the next century as the NAO moves into a stronger positive phase in response to global warming (Osborn 2004). Clearly, more

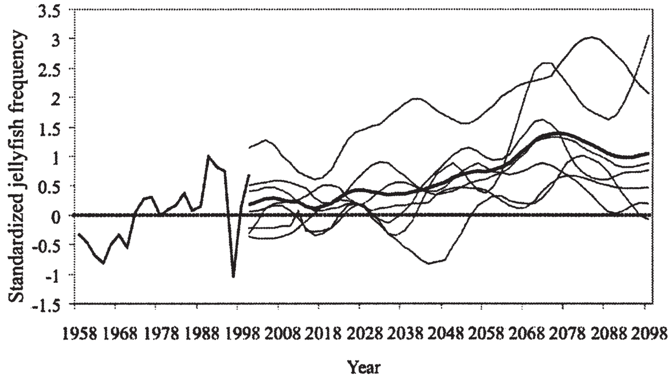

Fig. 3. Predicted exploratory trends in jellyfish frequency in west-central North Sea until 2100. NAOI-jellyfish model in Fig. 2a (initial solid line for existing data) coupled with outputs from NAOI predictions under seven climate change scenarios (Osborn 2004) (thin lines). Thick black line represents mean for the seven scenarios. Relative confidence level for these individual simulations is low (Osborn 2004), but accuracy is increased if a set of alternative models is used together to create a "consensus" projection (Araújo et al. 2005).

detailed mechanistic models are required, but are not possible on these data, so these projections have to be treated as preliminary. The evidence available from our study, however, suggests that projected climate change, including reducing ocean pH, may increase the frequency, and thus influence, of gelatinous predators in the North Sea over the next 100 yr.

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