Sandeel recruitment in the North Sea: demographic, climatic and trophic effects

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ABSTRACT: The lesser sandeel *Ammodytes marinus*, which is one of the most abundant fish in the North Sea, has highly variable recruitment dynamics. We evaluate potential associations between their recruitment and some key biological and physical factors. Population data were analysed at the North Sea scale (years 1983 to 1999) and at the regional scale (southwestern section and northeastern section; years 1984 to 1996/7). Relationships between recruitment and spawning stock biomass were weak, but Age-1 sandeels (non-spawners) were related negatively with recruitment, implying that demographic effects are important. A negative relationship was detected between recruitment and the winter index of the North Atlantic Oscillation, which affects sea temperatures during the egg and larval period. Warmer sea temperatures correlated with poorer than average recruitment. This effect was most pronounced in the southwestern part of the North Sea, which is near the southern limit of the species' distribution. There was a positive association between recruitment and *Calanus* copepod (Stages V and VI) abundance around the time of larval hatching, suggesting that the availability of this prey species is important for young sandeel survival. Our findings suggest that climate change may impact upon sandeel populations in the North Sea.

KEY WORDS: *Ammodytes* · *Calanus* · Climate · Larvae · North Atlantic Oscillation · Recruitment · Sandeel · Temperature

INTRODUCTION

Recruitment can be defined as the number of individuals in a population that reach a specified stage of an organism's life cycle (Jennings et al. 2001), and understanding the processes that control it is of fundamental importance to population biologists. In the context of commercial fisheries, a target species' recruitment is usually assessed as the number of individuals alive at the age when they first appear within the catches. Therefore, recruitment (to a closed population) depends upon the number of eggs that are produced by spawning adults, and the mortality rate of the eggs, larvae and juveniles between the time when they are laid and the age when they are first caught.

A common means of analysing the population dynamics of a fished species is to use population assessment records to generate predictions of recruitment, which are based upon the number of eggs thought to be produced in the population. Egg production can be calculated from estimates of spawner abundance, size, fecundity and number of spawning events, but often simply the spawning stock biomass (SSB) is instead used as a proxy for egg production. The relationship between recruitment and SSB can be described by various theoretical curves, which have inherent density-dependent assumptions controlling the non-linear association between recruitment and SSB. Well-known examples include the Beverton-Holt relationship (Beverton & Holt 1957), the Ricker relationship (Ricker 1954) and the Shepherd relationship

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(Shepherd 1982). Although these curves are extensively used for making recruitment predictions and setting landing limits, data are often scattered widely about these fitted curves.

In many marine fishes, egg production can be several orders of magnitude greater than recruitment due to the huge fecundity of spawners and the massive mortality suffered by early life stages. Thus, any factor that influences early life stage mortality can have profound effects upon recruitment, and can cause deviation about the SSB-recruitment curve. This realisation (Hjort 1914) has led to extensive fields of research into the biological and physical factors controlling mortality during early life stages in fishes.

Of the biological factors, predation threat and food availability are 2 of the principle processes that have received attention. Newly hatched larvae are especially vulnerable to predation due to their small size and poorly developed sensory and escape capabilities (Blaxter & Batty 1985, Blaxter & Fuiman 1990). In some species, cannibalism by older age classes may present an added source of predation, and in such cases, the demographic structure of population can have important consequences for juvenile survival (Bailey & Houde 1989). Food availability is also important because the juvenile stages have high development and per-unit-mass metabolic rates, which put them at risk of starvation unless sufficient prey is available soon after hatching (Cushing 1975, Pope et al. 1994). Physical factors (e.g. ocean currents, upwelling, turbulence and temperature) are important because they have direct effects upon larval growth, development and transport, and indirect effects via, for example, prey and/or predator abundance (e.g. Hayward 1997, Hofmann & Powell 1998, Hollowed et al. 2001).

In this paper, we evaluate the recruitment dynamics of the lesser sandeels *Ammodytes marinus* in the North Sea with respect to SSB, demographic structure of the population, climatic processes and zooplankton (prey) abundance. Sandeels are a key component of the North Sea ecosystem, forming an important trophic link between zooplankton production and higher predator species (Greenstreet 1996). A commercial fishery for sandeels (predominantly *A. marinus*) began in the 1950s and remained comparatively small (landings <200 000 t yr⁻¹) until the fishery started to expand rapidly in the early 1970s. Since the mid-1980s, annual landings have fluctuated about a mean of 820 000 t, ranging between 580 000 and 1 100 000 t (Anonymous 2001). No catch forecasts are made for the fishery because the recruitment dynamics are highly erratic. One reason for this is that the species is fairly short lived. Most individuals are sexually mature at 2 yr (Macer 1966, Gauld & Hutcheon 1990), and few survive beyond 3 to 4 yr because of their high natural mortality rate (Anonymous 2001). Thus, SSB is highly dependent upon recruitment in recent years.

Ammodytes marinus lay demersal eggs between November and January, and their planktonic larvae are present in the water column between late January and May (Henderson 1953, Reay 1970, Hart 1974). Thereafter, the juveniles settle onto seabed areas with course, sandy substrata (Wright et al. 2000). In the summer months, they form large schools in the water column during the daytime, feed on zooplankton and bury themselves within the substratum at night. With the onset of winter, they cease feeding and mostly remain buried until the following spring (Winslade 1974a,b,c).

Since the relationship between SSB and recruitment is very scattered in North Sea sandeels (Anonymous 2001, Arnott et al. 2002), the aim of this study was to test whether recruitment is affected by additional factors that might influence survival between the time of hatching and the time when 0-group fish first appear in the commercial catches (soon after they settle onto the seabed; Anonymous 2001).

The demographic structure of the sandeel population was explored because it has been postulated that non-spawning (1-group) sandeels may have density-dependent effects that are unaccounted for within the SSB-recruitment relationships (Furness 1999, Arnott et al. 2002). This is because 1-group sandeels are usually more numerous than the Age-2+ spawning sandeels (Anonymous 2001).

The main physical parameter we evaluate is the North Atlantic Oscillation (NAO). The NAO is a large-scale climatic phenomenon that influences wind, rainfall and temperature regimes throughout the North Atlantic and its surrounding land masses. Monthly indices of NAO are based upon the difference in normalised atmospheric pressures (at sea level) between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland. Positive winter indices (averaged over December to March) are known to correlate with strong winter storms crossing the Atlantic Ocean along northerly tracks, resulting in warmer, windier and wetter than average winters in the vicinity of the northeast Atlantic. Negative indices are associated with colder and drier winters (Hurrell 1995). The NAO has profound and widespread effects upon terrestrial, freshwater and marine ecosystems (e.g. Ottersen et al. 2001), and has been shown to have an influence across a number of trophic levels in the North Sea (e.g. Heyen et al. 1998, Reid et al. 1998, O'Brien et al. 2000, Thompson & Ollason 2001).

We have performed further analyses using sea temperature data, since the NAO winter index correlates positively with sea temperature during late winter and early spring in the North Sea (Becker & Pauly 1996) (i.e. the months when sandeel larvae are developing).

One expectation in this respect, might be that higher than average temperatures have a negative effect upon sandeel recruitment. This is because sandeels in the North Sea approach the southern limit of the species distribution (Reay 1970) and they are therefore near the warmer climatic extremes to which they are adapted. Under such circumstances, fish stocks are likely to have poorer than average recruitment in warm years (Myers 1998).

To test for potential relationships between food availability and recruitment, the effects of *Calanus* copepod abundance have been examined, since these are an important prey item for larval sandeels (Reay 1970). In particular, we hypothesise that, if feeding conditions are important, *Calanus* abundance during the larval stages should be positively associated with recruitment, since this would reduce the likelihood of starvation.

MATERIALS AND METHODS

Sandeel population data. Sandeel spawning stock biomass (S) in January, the number of 1-group sandeels in January (N_1) and the number of 0-group recruits in July (N_0) in the North Sea population as a whole were taken from the most recent single-species virtual population analyses (SSVPA) of sandeel fisheries data for the period 1983 to 1999 (Anonymous

2001). The data do not include Shetland sandeels (northwestern portion of North Sea), since this fishery is assessed separately. Recruitment of the 2000 year class was not included in the analyses because its calculation was based on limited landings and sampling (0-group fish only constitute a small proportion of the catch) and was very sensitive to model assumptions. As such, the 2000 datum was considered to be preliminary and an unreliable estimate of recruitment by the authors of the report (Anonymous 2001).

There is some evidence that North Sea sandeels comprise a number of sub-populations that have restricted mixing between them, rather than a single population (Procter et al. 1998). Although population assessments are usually reported at the whole North Sea level, SSVPA assessments for two of the main sub-populations identified by Procter et al. (1998) have been performed by Pedersen et al. (1999). Regional population data for Regions 1 and 2 were taken from these assessments covering the periods 1983 to 1996 and 1983 to 1997, respectively. Region 1 covers most of the North Sea area to the west of 4° E lying between 51 and 56° N. Region 2 covers most of the area to the east of 1° E lying between 55° 30′ N and 59° N (Fig. 1). For Region 2, N_0 in July was used as an estimate of recruitment (as above, with the whole North Sea data). For Region 1, no N_0 data were available, so instead N_1 in January the year after settlement was taken as a mea-

Fig. 1. Assessment areas. The whole North Sea sandeel assessment data cover Areas IVa, IVb and IVc, excluding the Shetland box. Temperature and zooplankton data are from Area IVb, where the majority of sandeels are caught. Regions 1 and 2 represent the areas considered in the population assessments of Pedersen et al. (1999). Numbers along axes indicate latitude and longitude
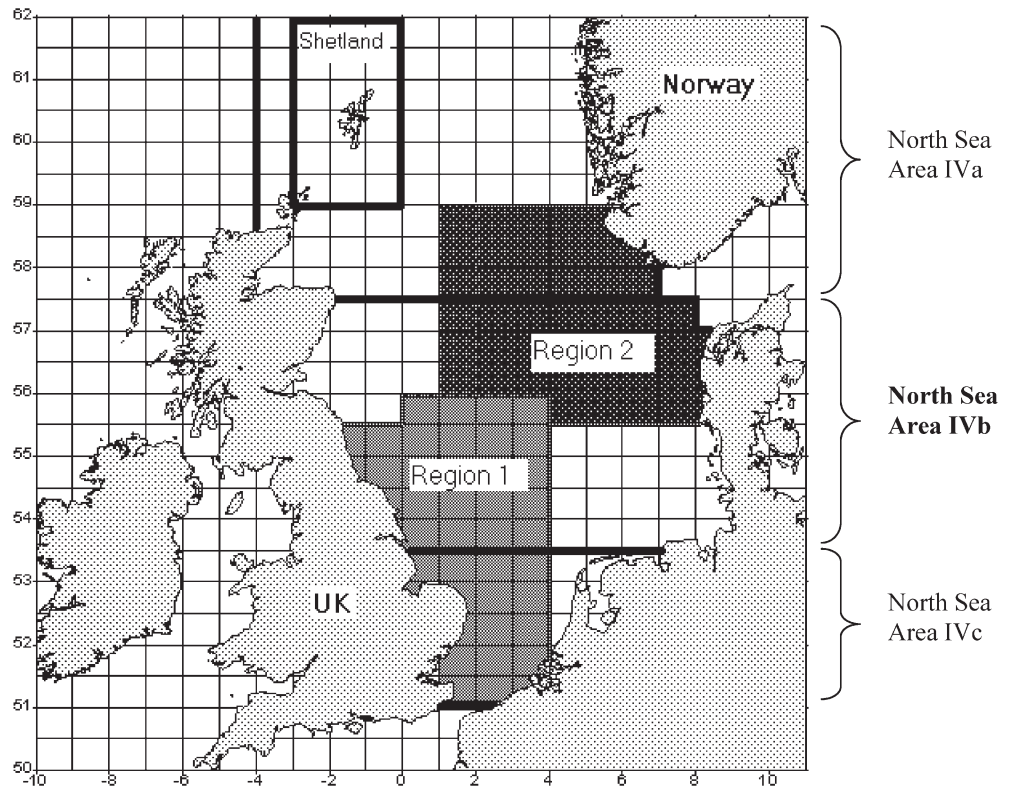
sure of recruitment (note that N_0 in July and N_1 the following January are highly correlated in the other assessments: for both the whole North Sea and Region 2, r > 0.99, p < 0.0001).

Climatic data. NAO winter indices (I_{NAO}, the mean of the December to March monthly indices) were obtained from the internet site of J. W. Hurrell at (www.cgd.ucar.edu/~jhurrell/nao.html#winter; also see Hurrell 1995). The values are based on the difference of normalised sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland, since 1864. The sea level pressure anomalies at each station that were used for calculating the indices were normalised by division of each seasonal mean pressure by the long-term mean SD (1864 to 1983).

Monthly mean sea bottom (T_b) and sea surface (T_s) temperature data were provided by the International Council for the Exploration of the Sea (ICES; Copenhagen, Denmark). Temperature data are averaged across ICES area IVb (spanning the central North Sea from 53° 30′ N to 57° 30′ N; see Fig. 1), which intersects Regions 1 and 2 and covers most of the intensely fished sandeel grounds in the North Sea (Anonymous 1999, Pedersen et al. 1999). Sea bottom and surface temperatures were investigated because the early life stages experience both water bodies (the eggs are demersal; the larvae are planktonic and undergo vertical migrations; the metamorphosed juveniles settle onto the seabed but feed in the water column).

Zooplankton data. Zooplankton data were provided by the Sir Alister Hardy Foundation for Ocean Science (Plymouth, UK), and covered 1983 to 1997 (data for 1998 and 1999 were not available). Monthly counts of *Calanus* Stage V and VI copepods (C_{v-vi}) were obtained from continuous plankton recorder surveys. The values used in the analyses are for ICES area IVb (as described above) and were $\log_{10}$ transformed.

Recruitment functions. Relationships between recruitment and spawning stock biomass were investigated using a Ricker function (Hilborn & Walters 1992). Coefficients were fitted by least-squared linear regression to the linearised version of the model:

$$\ln\left(\frac{N_0}{S}\right) \;=\; aS + k \qquad (1)$$

where N_0 is the number of recruits (billions), S is the spawning stock biomass (1000s of tonnes), and a and k represent fitted coefficients. The significance of each coefficient within the model was tested by *t*-test (Minitab v.13.31 software, Minitab).

Additional independent variables were added to the model by extending the Ricker function into a multiple regression (Hilborn & Walters 1992). The function used for modelling the effects of both S and N_1 abundance took the form:

$$\ln\left(\frac{N_0}{S}\right) \;=\; aS + b\ln(N_1 + 1) + k \qquad (2)$$

where N_1 represents 1-group abundance in billions (ln transformed to meet normality criteria). Further extension of the model to include an environmental variable took the form:

$$\ln\left(\frac{N_0}{S}\right) \;=\; aS + b\ln(N_1 + 1) + cE + k \qquad (3)$$

where E represents the environmental variable (e.g. I_{NAO} or temperature).

Correlation analyses. Autocorrelation coefficients of recruitment data and regression residuals were calculated according to Chatfield (1996). N_0 data were ln transformed in order to meet normality criteria.

Pearson product moment correlation coefficients were calculated from comparisons between recruitment data and 1-group abundance, and between recruitment data and environmental data (N_0 and N_1 data were ln transformed). Several series of correlations were generated between recruitment and monthly T_b, T_s and C_{v-vi} data, whereby recruitment was compared with the environmental measure of interest for each of the 12 mo prior to the year of recruitment, as well as the 12 mo covering the actual recruitment year (total of 24 mo, i.e. R_y vs $E_{1,y-1}$, R_y vs $E_{2,y-1}$ ..... R_y vs $E_{12,y}$ etc., where R_y represents a recruitment value for Year y and $E_{x,y}$ represents an environmental parameter during Month x of Year y). Values of R_y comprised either N_0 (ln transformed), or recruitment residuals from Eq. (2). We hypothesised that any correlations with environmental data from the months prior to egg laying (approximately January) might suggest indirect effects upon recruitment (e.g. by affecting parental gamete production and viability), whereas correlations during the egg/larval stage months would suggest more direct effects acting upon the young developmental stages. We did not expect to find any significant correlations after June of the actual recruitment year, since N_0 values in the population assessments are estimates of recruitment numbers in July. As recruitment data were correlated across 24 different months of environmental data within each correlation series, Type I errors were accounted for by applying a Bonferroni correction factor. Hence, the level of significance was adjusted to 0.002 (i.e. 0.05/24).

RESULTS

Relationship between recruitment and N_1

In all 3 of the population data sets, a significant negative correlation was found between N_0 and N_1 (both ln transformed). Correlation coefficients for the whole North Sea, Region 1 and Region 2 were −0.563 (p =

Table 1. Fitting of recruitment models for sandeels in the whole North Sea (1983 to 1999), Region 1 (1983 to 1996) and Region 2 (1983 to 1997). N_0 represents the number of recruits (billions), S is spawning stock biomass (1000s of tonnes), N_1 is the number of Age-1 sandeels ($\times 10^8$) in January and I_{NAO} is the North Atlantic Oscillation winter index. The values a, b, c and k are coefficients fitted to the model by least-squares linear regression. The significance of each coefficient was tested by t-test. In Region 1, N_1 was used as estimate of recruitment the year before — see 'Materials and methods'. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

Model	Coefficient	Fitted coefficients		
		North Sea	Region 1	Region 2
Eq. (1)	a	−0.0010*	−0.0018	−0.0038**
$\ln(N_0/S) = aS + k$	k	+0.5013	−0.8921	+0.7297*
Eq. (2)	a	−0.0016***	−0.0031*	−0.0040**
$\ln(N_0/S) = aS + b\ln(N_1 + 1) + k$	b	−0.7175**	−0.6953*	−0.6478*
	k	+5.008**	+2.396	+3.5420**
Eq. (3)	a	−0.0019***	−0.0042***	−0.0037**
$\ln(N_0/S) = aS + b\ln(N_1 + 1) + cI_{NAO} + k$	b	−0.8002***	−0.6277*	−0.5640*
	c	−0.1405**	−0.1963*	−0.1122
	k	+3.0662***	+2.739*	+3.277**

0.019, n = 17), −0.648 (p = 0.017, n = 13) and −0.568 (p = 0.034, n = 14), respectively.

Fitting the recruitment data according to Eq. (1) (S as the only independent variable) produced less satisfactory results than Eq. (2) (S and N_1 as independent variables) and revealed that the coefficient for $\ln(N_1 + 1)$ in Eq. (2) was significantly negative in all cases (North Sea: p = 0.007; Region 1: p = 0.026; Region 2: p = 0.025; see Table 1).

North Atlantic Oscillation

Direct correlations between N_0 (ln transformed) and I_{NAO} produced negative coefficients, but none differed significantly from 0 (North Sea: r = −0.355, p = 0.162; Region 1: r = −0.536, p = 0.059; Region 2: r = −0.317, p = 0.269).

Controlling for the effects of S and N_1 strengthened these negative relationships (I_{NAO} vs residuals from Eq. 2; North Sea: r = −0.601, p = 0.011; Region 1: r = −0.552, p = 0.050; Region 2: −0.492, p = 0.074). Thus, years with a strong positive I_{NAO} correspond with years in which recruitment is lower than expected.

The results from fitting the recruitment data according to Eq. (3) (S, N_1 and I_{NAO} as independent variables) reveal that the coefficient for I_{NAO} was negative in all instances, and was significant at the whole North Sea level (p < 0.01) and in Region 1 (p = 0.028), but not in Region 2 (p = 0.091; see Table 1).

Temporal periodicity of recruitment

The autocorrelation coefficients (Table 2) of the N_0 time series data (ln transformed), at a lag of 1 yr, were significantly negative for all 3 population data

sets, indicating that a strong recruitment year is generally followed by a weaker recruitment year, and vice versa. The residuals derived from the S model (Eq. 1) produced very similar results, but the lag-1 autocorrelations were no longer significant after the effects of N_1 were accounted for (residuals from Eq. 2). Residuals from the $S + \ln(N_1 + 1) + I_{NAO}$ model (Eq. 3) produced similar results to those from Eq. (2).

Sea temperature

For the period covered by our data (North Sea recruitment time series: 1983 to 1999), I_{NAO} was positively correlated with mean monthly sea bottom (T_b) and sea surface (T_s) temperatures during the first half of the year (Fig. 2A,E).

Comparisons betweexn sea temperature data and N_0 (ln transformed) produced 1 correlation that was significant at the Bonferroni corrected level (p = 0.002); in Region 1, T_s in April was negatively related to N_0 in the

Table 2. Autocorrelation coefficients, at a lag of 1 yr, for recruitment data from the whole North Sea, and from Regions 1 and 2. Values have been calculated using the normalised recruitment data ($\ln[N_0 + 1]$), and using residuals from recruitment Eq. (1) (S as independent variable), Eq. (2) (S and N_1 as independent variables) and Eq. (3) (S, N_1 and I_{NAO} as independent variables). *Autocorrelation coefficients significant at the 5% level or less

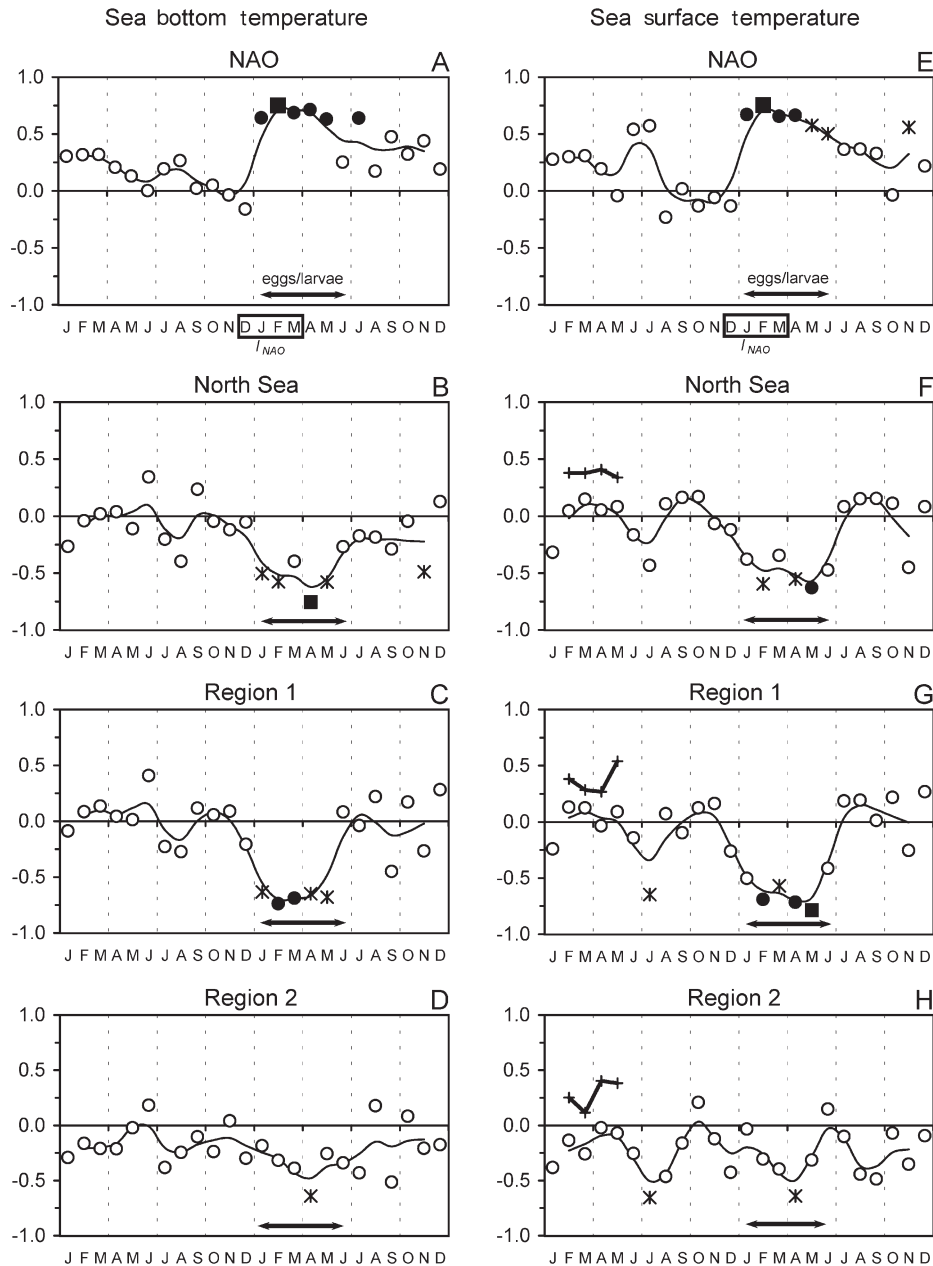|	$\ln(N_0 + 1)$	Eq. (1) residuals	Eq. (2) residuals	Eq. (3) residuals
North Sea	−0.52*	−0.55*	−0.04	−0.14
Region 1	−0.51*	−0.51*	−0.22	−0.31
Region 2	−0.48*	−0.44*	−0.14	−0.17

Fig. 2. Time series plots of Pearson product moment correlation coefficients (*y*-axis of each graph) from monthly sea bottom temperature (A–D) and sea surface temperature (E–H) data. Monthly temperatures covering the year prior to recruitment and year of recruitment (arrows indicate egg/larval phase) were correlated with: (A,E) I_{NAO} (North Atlantic Oscillation [NAO] winter index during boxed months) for the year of recruitment; (B,F) recruitment residuals from the whole North Sea population; (C,G) recruitment residuals from the Region 1 population; (D,H) recruitment residuals from the Region 2 population. The recruitment residuals were derived from Eq. (2) (i.e. having accounted for the effects of spawning stock biomass and 1-group sandeels). The p-value of each correlation coefficient is represented by its symbol: ○, $p > 0.05$; ✳, $p < 0.05$; ●, $p < 0.01$; ■, $p < 0.002$ (the Bonferroni corrected significance level is 0.002 in each instance). The fitted thin line is a centrally weighted 3-point moving average, inserted to show general month-to-month trends. (Four-point bold line plots in panels F to H show correlations between T_s and $\ln(N_0 + 1)$ data, rather than between T_s and Eq. (2) recruitment residuals; see 'Discussion' for more details)

same year (r = −0.763, p = 0.002). In general, across all 3 population data sets, correlations between T_b and N_0 and between T_s and N_0 produced coefficients that

were negative in every instance across the months February to May in the year of recruitment (total of 24 correlations, range of r values = −0.15 to −0.76).

An even clearer picture emerged after accounting for the effects on recruitment of both S and N_1 (residuals from Eq. 2; Fig. 2). These recruitment residuals produced stronger, more consistent correlations, coinciding with the egg and larval development period (predominantly January to May; Macer 1965, Langham 1971). Two significant relationships were detected with these residual data at the Bonferroni corrected 5% significance level (p = 0.002). North Sea recruitment was negatively correlated with T_b in April of the larval period (r = −0.755, p < 0.001), and Region 1 recruitment was negatively correlated with T_s during April (r = −0.786, p < 0.001). Overall, at both the North Sea and regional scales, the larval months coincided with periods of persistent negative correlations between recruitment and temperature. This effect was most pronounced in Region 1 and least pronounced in Region 2.

These results are summarised by the fact that, for the North Sea and Region 1, residuals from the $S + \ln(N_1 + 1)$ model (Eq. 2) correlated negatively with sea temperatures averaged across the egg/larval months of January to May (North Sea residuals, for T_b: r = −0.561, p = 0.019, for T_s: r = −0.569, p = 0.017; Region 1 residuals, for T_b: r = −0.668, p = 0.013, for T_s: r = −0.732, p = 0.004; but in Region 2 residuals, for T_b: r = −0.367, p = 0.197, for T_s: r = −0.402, p = 0.154; see Fig. 3).

Outside of the egg/larval period, a weak relationship between $S + \ln(N_1 + 1)$ residuals (Eq. 2) and T_s in July of the year prior to recruitment was found (Fig. 2F−H). This effect was strongest in Region 2 (r = −0.653, p = 0.011).

Calanus **zooplankton**

Both N_0 data and $S + \ln(N_1 + 1)$ residual data (Eq. 2) were compared against C_{v-vi} monthly counts covering the year before and the year of recruitment. The 2 sets of recruitment proxies produced similar results, with the main correlation trends being strengthened after accounting for S and N_1. The correlations with $S + \ln(N_1 + 1)$ residuals (Fig. 4A−C) reveal a tendency towards positive relationships with C_{v-vi} during early stages of the egg/larval period. In Region 1, a strong positive relationship was found during February (r =

+0.861, p < 0.001; cf. Bonferroni correction at 5% level: p = 0.002). A slightly weaker correlation was found in the North Sea during February (r = 0.734, p = 0.003), whereas no strong correlations were detected in Region 2.

Tests were performed to see whether C_{v-vi} over the egg/larval months of January to May was related to I_{NAO} or monthly T_s. No significant correlations were detected with I_{NAO} (0.08 < p < 0.91). With T_s, a negative relationship was found in February (r = −0.578, p = 0.030, n = 14 yr of data) and a positive relationship in April (r = 0.660, p = 0.007).

Since T_s and C_{v-vi} may be related to one another as well as to sandeel recruitment, a series of month-by-month regression analyses was performed in which both T_s and C_{v-vi} data from the month of interest were included as environmental parameters in Eq. (3). Either or both parameters were removed from the
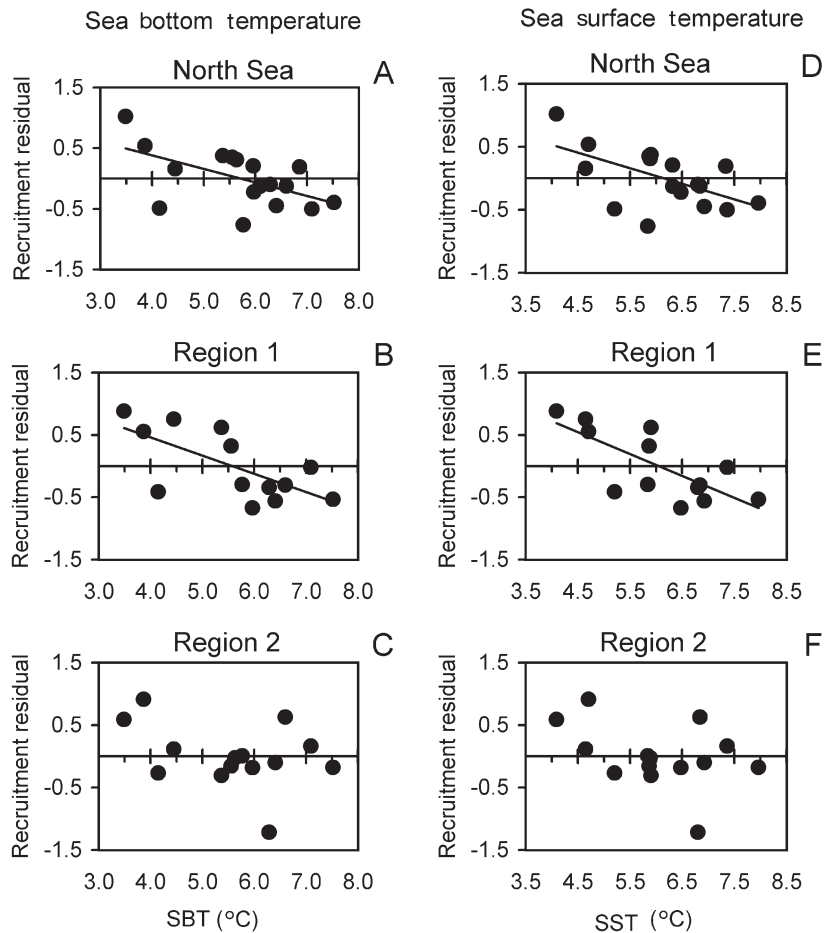

Fig. 3. Relationships of sandeel recruitment with sea bottom temperature (left-hand panels) and sea surface temperature (right-hand panels) data. Recruitment is expressed in terms of residuals from Eq. (2) (i.e. having accounted for the effects of spawning stock biomass and 1-group sandeels). (A,D) Whole North Sea recruitment; (B,E) Region 1 recruitment; (C,F) Region 2 recruitment. Fitted lines (linear regressions) are included in cases where the relationships were found to be significant
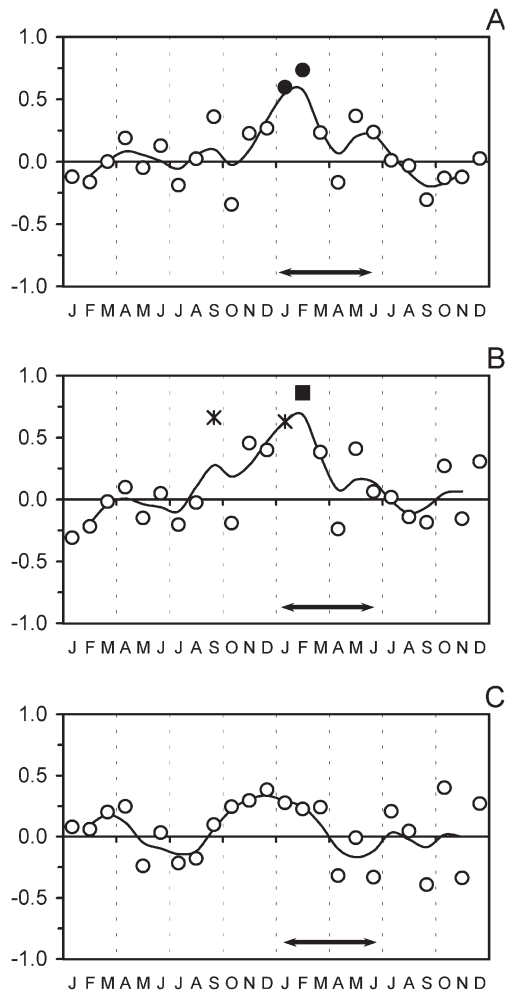
Fig. 4. Time series plots of Pearson product moment correlation coefficients (*y*-axis of each graph) derived from monthly *Calanus* Stage V and VI counts. Monthly counts from the year prior to recruitment, and the year of recruitment (arrows along the *x*-axis show the egg and larval period), were correlated with recruitment residuals from Eq. (2) (accounting for the effects of spawning stock biomass and 1-group sandeels). (A) Recruitment to the whole North Sea. (B) Recruitment to Region 1. (C) Recruitment to Region 2. The p-value of each correlation coefficient is represented by its symbol: ○, p > 0.05; ✱, p < 0.05; ●, p < 0.01; ■, p < 0.002 (the Bonferroni corrected significance level is 0.002 in each instance). The fitted line is a centrally weighted 3-point moving average, inserted to show general month-to-month trends

regression if their coefficients were found to be non-significant (*t*-test). Interactive terms were also tested in the model, but were not found to be significant. The analyses (Table 3) indicate that, in the North Sea and Region 1, $C_{\text{v-vi}}$ is a significant factor around the time of hatching (January to March), but that T_{s} is of more importance later on in development, between March and May. In Region 2, $C_{\text{v-vi}}$ was never significant and T_{s} only had a comparatively weak effect during April.

DISCUSSION

Our analyses indicate that the spawning stock biomass, by itself, is a poor predictor of sandeel recruitment in the North Sea, and suggest that additional influences are exerted by environmental conditions and the demographic structure of the population. Recruitment was negatively related with sea temperature during the egg/larval stages, negatively related with the number of aged 1 sandeels (which comprise the majority of the population; Anonymous 1999) and positively related with feeding conditions during the egg/larval stages.

The sandeel population assessments performed by ICES calculate *S* on the assumption that Age-2+ sandeels all spawn and that none of the N_1 sandeels spawn. However, it is known that a proportion of N_1 sandeels may in fact spawn, whereas not all of Age-2+ fish necessarily do so (Macer 1966, Gauld & Hutcheon 1990). Since ca. 40 to 80% of the total stock biomass typically comprises N_1 in the first half of the year (Anonymous 1999), fairly large errors in estimating *S* may arise. This may partly explain the lack of relationship between *S* and recruitment, but the other effects that we have detected here are probably of greater importance in explaining the observed variability.

The negative relationship between N_1 and recruitment implies that density-dependent processes are taking place within the population, but the mechanism(s) by which these occur remain unclear. Since the demersal egg stages are laid within the sediment of the seabed, and sandeels apparently have no distinctly separated spawning grounds (Reay 1970), the eggs might be disrupted by the burying behaviour of established sandeels or cannibalised when they hatch. Alternatively, cannibalism and competition for seabed space and food could be important when the larvae settle from the plankton. Translocation of larvae from one area of seabed to another is thought to be the main means of inter-population mixing in sandeels because the adults are non-migratory (Procter et al. 1998). Therefore, understanding the meta-population dynamics of sandeels will require further studies into the proximate causes of density dependence at different stages of the sandeel lifecycle.

The autocorrelation coefficients produced from the recruitment analyses (Table 2) show interesting trends that shed light on sandeel recruitment processes. Both the actual recruitment data (N_0) and residuals from the *S* model (Eq. 1) produced significant negative autocorrelations at a lag of 1 yr. This was true in all cases, both at the whole North Sea and regional level. However, once the influence of N_1 had been taken into account (by examining residuals from the $S + \ln[N_1 + 1]$ model, as well as the $S + \ln[N_1 + 1] + I_{\text{NAO}}$ model), the effect was no

longer significant. This suggests that the density-dependent effects imposed by the N_1 sandeels are largely responsible for the alternating years of high and low recruitment. Intuitively, this makes sense, since a year of high recruitment results in high N_1 the following year, which will then compete with new arrivals. Modelling studies on rainbow smelt *Osmerus mordax* populations in Lakes Ontario and Erie support this notion (Lantry & Stewart 2000). These authors found that fluctuating years of high and low recruitment could be explained by cannibalistic behaviour of Age-1+ fish, even when this mode of feeding behaviour operated at very low levels. Since adult sandeels are known to consume fish larvae (Reay 1970), cannibalism may explain the effects of 1-group sandeels that we detected.

The ecological effects of the NAO have been receiving increasing attention in recent years. There is strong evidence that during the winter and spring in northwest Europe, terrestrial, freshwater and oceanic conditions are closely associated with the atmospheric parameters incorporated within I_{NAO} (Hurrell 1995) and that these influence ecological processes (e.g. Ottersen et al. 2001). In the North Sea, a positive link between sea temperature anomalies and I_{NAO} were identified by Becker & Pauly (1996), an effect also evident with our data (Fig. 2A,E). Moreover, we detected a negative relationship between I_{NAO} and sandeel recruitment in the North Sea during the period from 1983 to 1999. I_{NAO} may affect recruitment through a variety of mechanisms, but our results indicate that, whatever processes are responsible, they operate predominantly upon the egg and/or larval stages. Recruitment proxies were negatively related with both T_b and T_s during the egg/larval phases, with the general effect of T_s being stronger than T_b (Fig. 3). These relationships disappeared abruptly after larval settlement (Fig. 2B–D,F–H), which contrasts with the more gradual diminishment of relationships between I_{NAO} and temperature during and beyond the egg/larval phase (Fig. 2A,E). Climatic factors during the early life stages of fishes have long been implicated as a cause of recruitment fluctuations. Around the UK, for example, plaice *Pleuronectes platessa* and dab *Limanda limanda* recruitment correlates negatively with sea temperature (Henderson 1998, Fox et al. 2000).

Myers (1998) noted that climatic correlations with recruitment often breakdown as subsequent years of data are accumulated, except in populations near the latitudinal limit of a species' range, where the relationships tend to remain robust with time. This suggests that the temperature effects we have detected here are of importance because the strongest influences were in the most southerly population (Region 1) and the effects were in the expected direction (i.e. poorer recruitment when conditions were warmer than usual). Region 1 (51 to 56° N) lies close to the southern (equatorial) limit of *Ammodytes marinus*, which inhabits latitudes of between 49 and 73° N (Reay 1970). In Region 2 (55 to 59° N), the climatic trends were weaker, but in the same direction as Region 1 (since the area still lies within the more equatorial half of the species' distribution). At the whole North Sea level, the strength of the climatic effects was intermediate, reflecting the fact that the data mainly integrate across both regions. The only exception to this was the weak negative link we detected between recruitment and T_s during July of the year preceding recruitment (Fig. 2F–H). This relationship was strongest in Region 2, thus reversing the trend that might otherwise be expected. However, sea surface temperature satellite images (http://www.bsh.de/Oceanography/Climate/Actual.htm) reveal that, although Region 2 is generally cooler than Region 1 during the egg/larval period of the year, it is actually warmer during the summer months. This would explain the reversal, and perhaps indicates that the fitness of the parental fish is in some way compromised by excessive summer temperatures.

Temperature has the potential to influence the development of eggs and larvae directly by affecting their developmental patterns, growth rates and behavioural responses (e.g. Cushing 1995, Temple & Johnston 1997, Johnston et al. 1998). Recruitment may also be affected by changes in the trophic structure of the

Table 3. Results of regression analyses, performed on a month-by-month basis, examining the dependence of recruitment upon sea surface temperature (T_s) and *Calanus* Stage V and VI copepod abundance (C_{v-vi}) during the sandeel larval period. For each month, a multiple regression was performed (Eq. 3) that included both monthly T_s and C_{v-vi} data as 2 separate environmental parameters. They were eliminated from the model if their regression coefficient was not significant (*t*-test, p > 0.05), and retained if it was significant (*S* and N_1 were always significant terms in Eq. 3 and were therefore always retained). Analyses were performed on recruitment data from the whole North Sea, Region 1 and Region 2. The values shown are p-values (*t*-test) of each coefficient that was retained. ns: non-significance

| | North Sea | | Region 1 | | Region 2 | |
	T_s	C_{v-vi}	T_s	C_{v-vi}	T_s	C_{v-vi}
Jan	ns	0.023	ns	0.036	ns	ns
Feb	ns	0.007	ns	0.001	ns	ns
Mar	ns	ns	0.006	0.043	ns	ns
Apr	0.032	ns	0.013	ns	0.014	ns
May	0.012	ns	0.002	ns	ns	ns
Jun	ns	ns	ns	ns	ns	ns

ecosystem, either with respect to the feeding conditions experienced by the larvae (bottom-up responses) or predation threat (top-down responses); these processes are not mutually exclusive (Roff et al. 1988).

The occurrence of bottom-up effects was supported by the positive association we found between $C_{v\text{-}vi}$ and sandeel recruitment. *Calanus* is an important dietary item of sandeels (Reay 1970), and although Stage V and VI *Calanus* are probably too big to be eaten themselves by the smallest sandeel larval stages, their abundance provides a direct estimate of immediate *Calanus* nauplii production potential. We detected few strong associations between climatic factors and $C_{v\text{-}vi}$, but the data we analysed were averaged across all of North Sea Area IVb and did not distinguish between different species of *Calanus*, which respond differently to climatic signals. I_{NAO} has been shown to influence oceanic inflow, primary production and zooplankton communities in the North Sea (Fromentin & Planque 1996, Planque & Fromentin 1996, Heyen et al. 1998), and therefore one would expect it also to affect the feeding conditions experienced by planktivores such as sandeels.

Sherman et al. (1981) attributed a rising abundance of sandeels on the opposite (northwest) side of the Atlantic to the over-exploitation of herring and mackerel (both sandeel predators), implying that top-down effects were dominant within the system. In the North Sea, herring are important predators of sandeel larvae (Hardy 1924), but tend to occupy more northerly areas during warm years (Corten 2001), which suggests that they were not responsible for the effects we detected, since the negative influence of warm conditions was most noticeable in the southern part of the North Sea (Region 1). Other means of top-down control may occur, however, and since this mechanism can have profound effects upon ecosystems (e.g. Verity & Smetacek 1996, Post et al. 1999), it should not be discounted.

The response of pathogens to climatic regime may also be important, and although this mechanism may be of relevance to fish recruitment (Henderson 1998), standard fishery assessment methods do not investigate the year-to-year variation in fish health status, making it impossible to evaluate the role of pathogens.

It is also possible that the mechanism of climatic perturbation differs between regions, or from year-to-year. Hart (1974) proposed that temperature anomalies and the extent of Atlantic water penetration into the North Sea between 1948 and 1968 affected the sandeel larvae abundance measured in the concurrent continuous plankton recorder surveys. However, the implied relationships were not always in agreement with one another, indicating that responses may differ in time and space. With our data, residuals from the $S + \ln(N_1 + 1)$ model (Eq. 2) in Region 1 correlated more strongly with mean T_s over the period from January to May

than with I_{NAO}, whereas in Region 2 the reverse situation was true. Thus, temperature may be a more important proximate cause in Region 1, whereas more indirect routes predominate in Region 2.

Two of the main influences upon sandeel recruitment that we detected (the demographic structure of the population and climatic conditions) could have an interesting counter-active behaviour. If warm conditions lead to lower recruitment than might otherwise be expected, they will also lead to lower N_1 numbers the following year, thus reducing the density-dependent effects among subsequent recruits. In other words, if y represents any given year, $T_{s,y}$ (this year's egg/larval phase sea surface temperature) may indirectly affect $N_{0,y+1}$ (next year's recruitment) via its effects upon $N_{0,y}$ (this year's recruitment). If true, one would expect the following: (1) Positive correlations should exist between $T_{s,y}$ and $N_{0,y+1}$; and (2) This positive association should disappear after accounting for the effects of $N_{1,y+1}$ (i.e. by testing the residuals from Eq. 2). We tested whether $T_{s,y}$ correlations during the months of February to May were significantly more positive with respect to $N_{0,y+1}$ than with respect to residuals from Eq. 2 (i.e. do the points along the bold lines in Fig. 2F to H lie significantly above the open circle points of the same month?). In each instance, we detected a significant difference, thus supporting the hypothesis that $T_{s,y}$ positively influences recruitment in Year $y+1$ via its effects upon $N_{1,y+1}$ (paired *t*-test comparison between February and May monthly correlation coefficients, North Sea: $t_3 = 12.67$, p < 0.0001; Region 1: $t_3 = 6.19$, p = 0.003; Region 2: $t_3 = 14.37$, p < 0.0001). Similar types of demographic/climatic interactions have been postulated in other species, such as the bass *Dicentrarchus labrax* (Henderson & Corps 1997).

Current climate models predict that global conditions will become warmer over the next century (Crowley 2000, Stott & Kettleborough 2002). Furthermore, it has been proposed that long-term warming of tropical waters, caused by human activity, has played an important role in driving the NAO towards an extreme positive phase during the last half century (Hoerling et al. 2001). Since climate forcing can have major effects upon fish populations (e.g. Finney et al. 2002), an obvious question leading on from our findings is: What effects will long-term changes in climate have upon sandeel populations in the North Sea, and the higher predators that feed on them? One expectation is that the southern limit of the species' distribution could shift northwards if conditions become warmer. With regard to sandeel fishing practices, sustainable harvest limits in the North Sea may decline with time if recruitment becomes compromised by rising temperatures, especially in more southerly areas (O'Brien et al. 2000). Identifying the proximate mecha-

nisms by which temperature affects sandeel recruitment, particularly during the egg and larval stages, will assist in understanding such responses and making informed management decisions.

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