Recruitment of lesser sandeel *Ammodytes marinus* in relation to density dependence and zooplankton composition

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ABSTRACT: Recent recruitment failure of lesser sandeel *Ammodytes marinus*, a key prey fish in the North Sea, followed by several years of low spawning stock biomass, prompted us to investigate factors influencing the recruitment of this species. We tested 2 hypotheses that relate to ecological mechanisms of recruitment regulation in lesser sandeel: (1) a positive spawning stock–recruitment relationship is decoupled in years associated with high abundances of age-1 sandeels and (2) the survival success of early larvae depends specifically on the abundance of *Calanus finmarchicus* and not *C. helgolandicus*. The findings of the present study supported both hypotheses and resulted in a multiple linear recruitment model with pronounced predictive capabilities. The model includes interactions between age-1 abundance and spawning stock biomass, plus the effect of *C. finmarchicus* abundance, and it explained around 65 % of the inter-annual variation in recruitment in contrast to only 12 % by a traditional Ricker curve. We argue that early egg production in *C. finmarchicus* supports the survival of larvae, and that climate-generated shifts in the *Calanus* species composition lead to a mismatch in timing between food availability and the early life history of lesser sandeels.

KEY WORDS: *Ammodytes marinus* · Recruitment · *Calanus finmarchicus* · Match/mismatch hypothesis · Density dependency · Climate change

INTRODUCTION

In many ecosystems sandeel is a key prey fish linking trophic levels (Furness 1990, 2002, Hain et al. 1995, Frederiksen et al. 2005). The lesser sandeel *Ammodytes marinus* constitutes the vast majority of sandeels in the North Sea and one of the largest fish biomasses (Temming et al. 2004, ICES 2005), and has supported a large industrial fishery since the 1950s. The Danish fleet alone harvested between 500 000 and 900 000 t of sandeels every year during the peak of the fishery in the 1990s. Variability in the abundance of lesser sandeels is thus likely to have broad effects on the entire ecosystem and the fisheries. The number of young-of-the-year sandeels settling into adult aggregations was historically low in 2002, and, subsequently, the spawning stock biomass came to a critically low level. This drastic reduction in population size has made development of new forecast methods and identification of factors affecting sandeel population dynamics high priorities (ICES 2007).

Adult lesser sandeels (age-1 and older) are found in large parts of the North Sea, with a distribution closely related to well-oxygenated bottom substrates consisting of gravel or coarse sand, and water depths between 20 and 100 m (Reay 1970). They bury in the sand, when water temperature or prey abundance is low (Winslade 1974a,c), and at night when low light intensity limits

prey visibility (Winslade 1974b). They reach sexual maturity at around age-2 and subsequently spawn in December/January (Macer 1966, Bergstad et al. 2001). The eggs stick to the substrate until they hatch during February and March (Macer 1965, Wright & Bailey 1996), whereupon larvae are found in most of the water column (Conway et al. 1997). After metamorphosis they settle in sandy seabeds into the aggregations of adults. Sandeel recruitment is traditionally defined as the amount of post-settlement individuals in June. Consensus has been reached that after settling individuals show high site fidelity (e.g. Gauld 1990, Pedersen et al. 1999).

Fish populations, particularly of species with a short lifespan such as the sandeel, are highly sensitive to variation in recruitment. In general, predation and starvation mortality during early life stages is massive, but decreases rapidly with increasing size. Consequently, recruitment success largely depends on the growth rate experienced by the larvae. Varying availability of suitable prey in time and space, during early life history will therefore contribute to variation in recruitment (Cushing 1990).

It is well documented that zooplankton availability during the larval stage is critical for the recruitment of lesser sandeel (Arnott & Ruxton 2002, Frederiksen et al. 2006) and of various other North Sea fish species (Economou 1991, Munk 1997, Gaard & Reinert 2002). In the analysis conducted by Arnott & Ruxton (2002), abundances of *Calanus* spp. Stage V and VI copepods in February were significantly related to recruitment of lesser sandeel. Arnott & Ruxton (2002) argued that lesser sandeel larvae in February and March are too small to prey on Stage V and VI copepods and instead prey upon copepod eggs. *Calanus* spp. copepods are dominant components of the zooplankton community in the North Sea, and consist mainly of *C. finmarchicus* and *C. helgolandicus*. Spring egg production of *C. helgolandicus* reaches its maximum in May, whereas egg production by *C. finmarchicus* peaks in March at around 37 eggs female^{-1} d^{-1} in the shelf waters (Jónasdóttir et al. 2005). In addition, a proportion of the high production of *C. finmarchicus* eggs in the slope water drifts into the North Sea (Richardson et al. 1999). The early *C. finmarchicus* egg production coincides with the hatching of sandeel eggs. Back calculation in larval otoliths has established the hatch date of sandeels in Shetland waters to be between mid-February and early April (Wright & Bailey 1996), and early larval stages (<6 mm) of sandeels have been observed in the continuous plankton recorder (CPR) in the North Sea between mid-February and the end of March (reported in Wright & Bailey 1996). Therefore, a shift from a *C. finmarchicus*-dominated community to a *C. helgolandicus*-dominated community is likely to cause a mismatch between the timing of prey availability and critical larval stages.

Carrying capacity refers to the maximum population size that can be sustained by resources within a habitat. Density dependence refers to population-regulating mechanisms inflicted by the population itself, for example, cannibalism or competition for habitat and food resources (Murdoch 1994).

Lesser sandeel is a non-migratory residential species associated with a defined habitat surface area, in which the spatial distribution of adults and juveniles overlap. These species characteristics favour the occurrence of density dependence and decoupling of the spawning stock–recruitment relationship when population size approaches carrying capacity.

The traditional way to account for density dependence and carrying capacity is by forcing non-linearity into the spawning stock–recruitment relationship. The Ricker stock–recruitment function (Ricker 1954) is one of various non-linear descriptions of this. Arnott & Ruxton (2002) applied the Ricker stock–recruitment function to model the recruitment of lesser sandeels. However, their results suggested that the main factor inducing density dependence was not the spawning stock size, but the quantitatively dominant premature age-1 population, which is not accounted for in a traditional Ricker function.

In the present study we have extended the analyses done by Arnott & Ruxton (2002), in order to further improve our understanding of the mechanisms involved in the recruitment regulation of lesser sandeels. To do this we used an updated time series, species-specific availability of copepods in the genus *Calanus* and interactions (non-additive effects) between the size of the age-1 population and the spawning stock biomass to model the recruitment of lesser sandeels in the North Sea. The winter NAO index (mean of the North Atlantic Oscillation index between December and March) has been included in the analysis to account for the climate/temperature effect reported by Arnott & Ruxton (2002).

We consider the 2 following hypotheses:

Hypothesis 1: The spawning stock–recruitment relationship is decoupled in years associated with high age-1 sandeel abundances.

Hypothesis 2: The survival success during early larval stages depends on the abundance of *Calanus finmarchicus* and not of *C. helgolandicus*.

MATERIALS AND METHODS

Data series. Population data for the North Sea sandeel *Ammodytes marinus* in ICES Division IV from 1983 to 2006 were taken from ICES seasonal stock assessments (ICES 2007). These data included spawning stock biomass (SSB) per million tonnes, and the

numbers of recruits (N_0) and age-1 individuals (N_1) in billions. SSB and N_1 represent age-2+ and age-1 abundance in January, and are based on catch data. N_0 represents the number of age-0 juveniles (the cohort produced by the SSB in January) in the second half of the year, and is a virual population analysis-type backward calculation based on age-1 sandeel catches in the subsequent year and survey data (tuning data).

North Sea zooplankton data were sampled by the CPR program in the section of the North Sea referred to as ICES Division IVb, and provided by SAHFOS (Johns 2008). Data consisted of species-specific mean abundance (numbers m^{-3}) in February of Stage V and VI calanoid copepods. The time series (1983 to 2006) used were: *Calanus finmarchicus* (FIN$_{Feb}$), *C. helgolandicus* (HEL$_{Feb}$) and the combination of both (CAL$_{Feb}$).

The winter North Atlantic Oscillation index (NAO$_{DJFM}$), calculated as mean monthly values from December through March from the website of Jim Hurrell (www.cgd.ucar.edu/cas/jhurrell, accessed 7 February 2008) was used as a proxy for variation in climate.

Data analysis and modelling. Different modelling frameworks were applied to test Hypotheses 1 and 2: (1) a traditional Ricker stock–recruitment function with inherent density dependence (Ricker 1954) and (2) statistical model frameworks in the form of general additive modelling (GAM) and linear regression modelling (LM). GAM was used to statistically test non-linear relationships. The lm-, gam- and nls-functions of the programming environment R (R Development Core Team 2007; with the mgcv library; Wood 2006) were used to fit the respective models. LM and GAM were applied with a Gaussian distribution, and GAM was applied using penalized regression splines with smoothing parameters selected by generalized cross-validation (GCV) with shrinkage (fixed to a maximum of 4 degrees of freedom).

The Ricker stock–recruitment function with the inclusion of an extra explanatory variable was formulated as $N_0 = a\text{SSB} \times \exp(-g\text{SSB}) + \exp(X)c$, where a, g and c represent fitted coefficients. The term $\exp(X)c$ is optional, and X can be any given additional explanatory variable. The function was fitted using nls, which determines the non-linear, least-squares estimates of the parameters.

The initial models were fitted to data series of N_1 and SSB as explanatory variables and N_0 as an independent variable. Non-additive effects related to interactions between SSB and N_1 were accounted for in the models. Explanatory variables or interaction terms that did not contribute significantly to the model ($p < 0.05$, F-test) were excluded, and the model parameters were re-estimated. The environmental drivers (NAO$_{DJFM}$, CAL$_{Feb}$, FIN$_{Feb}$ and HEL$_{Feb}$) were subsequently added one by one to test whether they contributed significantly to the model.

Akaike's information criterion (AIC, Akaike 1974) takes into account the number of parameters in the model and was used to compare goodness of fit; r^2 was used as a measure of the amount of inter-annual variation in N_0 explained by the model.

Bootstrap-based cross validation with 1000 iterations was used to confirm the reliability of the final best model. During each iteration, 12 of the 23 yr in the time series were used to train the model, and predictions were made for the remaining 11 yr. Pearson's product moment correlation coefficient was used to express the prediction error for each iteration; therefore, the larger the correlation coefficient the smaller the prediction error.

For correlation analyses outside the models, correlation coefficients (r) and p-values (p) were calculated using the Pearson's product moment correlation analysis with Spearman's test.

RESULTS

Initial fitting attempts and 1996

Initial fits indicated that the model was extremely sensitive to 1 particular year in the data series, 1996. This year was associated with an unusual high N_0 of 1936 billion, which was 700 billion more than the second largest number in the entire time series. This unusually large N_0 coincided with an unusually low NAO$_{DJFM}$ and an extremely cold winter. Including NAO$_{DJFM}$ as an explanatory variable in the LM resulted in parameter estimates driven solely by 1996 (Cook's distance = 1.931). The subsequent analyses were conducted without 1996.

Density dependence

To test Hypothesis 1, that the spawning stock–recruitment relationship is decoupled in years associated with high abundances of age-1 sandeel *Ammodytes marinus*, recruitment modelling based on SSB, N_1 and their interactions was performed.

The smoothing parameters of a GAM fitted with additive effects were insignificant (p ~ 0.15). It was not possible to include interactions because these consumed too many degrees of freedom.

The LM allowed for inclusion of interactions. The interaction between SSB and N_1 was significant (p = 0.029), and 30% of the inter-annual variation in N_0 could be explained by this model (Table 1; Eq. 1a). It was therefore concluded that the LM framework was adequate for the purposes of the present study.

The traditional Ricker function explained 12% of the inter-annual variation in N_0 and was not significantly

Table 1. Model results. a, b, c, g and k represent coefficients fitted to the model by least-squares linear regression; the given values are p-values used to evaluate whether the estimated coefficient differed significantly from 0. Akaike's information criterion (AIC) is given to compare model fits; r^2 reflects the amount of variation explained by the fit: $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; p-values for coefficients in the Ricker function are not directly comparable with p-values from linear regression modelling (LM) and general additive modelling (GAM) coefficients. For all other abbreviations see 'Materials and methods: Data series'

| Models | Fitted coefficients (p-values) | | | | | Comparison of models | |
	k	a	b	c	g	r^2	AIC
Eq. (1a) LM $N_0 = a\mathrm{SSB} + bN_1 + g(\mathrm{SSB} \times N_1) + k$	0.5	0.018*	0.078		0.029*	0.302	325.7
Eq. (1b) LM $N_0 = a\mathrm{SSB} + bN_1 + c\mathrm{FIN}_{\mathrm{Feb}} + (g\mathrm{SSB} \times N_1) + k$	0.824	0.005**	0.023*	<0.001***	0.008**	0.649	311.9
Eq. (2a) Ricker $N_0 = a\mathrm{SSB} \times \exp(-g\mathrm{SSB}) + \exp(N_1)c$		0.001**		0.376	0.001**	0.154	328.1
Eq. (2b) Ricker $N_0 = a\mathrm{SSB} \times \exp(-g\mathrm{SSB})$		<0.001***			0.001**	0.119	327.1
Eq. (2c) Ricker $N_0 = a\mathrm{SSB} \times \exp(-g\mathrm{SSB}) + \exp(\mathrm{FIN}_{\mathrm{Feb}})c$		0.008**		<0.001***	0.006**	0.501	328.1

improved by adding N_1 as an additional explanatory variable (Table 1; Eq. 2a,b).

The significant interaction between SSB and N_1 was explored more closely. This was done by disaggregating the data into 3 subsets of equal sizes according to age-1 abundances of the respective years — Subset 1: <145 billion age-1 individuals, Subset 2: between 145 and 275 billion age-1 individuals and Subset 3: >275 billion age-1 individuals. A significant positive linear relationship ($r = 0.794$, $p = 0.019$) existed between N_0 and SSB when age-1 abundance was low (Subset 1), while at high numbers (Subsets 2 & 3), no relationship was found (Fig. 1).

In summary, we propose a linear recruitment model which accounts for interactions between spawning stock biomass and age-1 abundance. The results support Hypothesis 1 by showing that: (1) a linear recruitment model, which includes the SSB–N_1 interaction, performs better than a linear model accounting for only additive effects and the traditional Ricker function and (2) that SSB is positively correlated to N_0, only when years of high N_1 were excluded.

Species-specific *Calanus* abundance and the NAO

During this stage of the analysis we tested Hypothesis 2 that the survival success of early larvae depends specif-

ically on the abundance of *C. finmarchicus* and not *C. helgolandicus*.

The environmental drivers ($\mathrm{FIN}_{\mathrm{Feb}}$, $\mathrm{HEL}_{\mathrm{Feb}}$, $\mathrm{CAL}_{\mathrm{Feb}}$ and $\mathrm{NAO}_{\mathrm{DJFM}}$) were added one-by-one to the Ricker function and LM (Table 1; Eqs. 1a & 2a). Only $\mathrm{FIN}_{\mathrm{Feb}}$ contributed significantly to the models, and the estimated coefficients were positive (Table 2). The variation explained by the models increased in the LM from 30 to 65 % and in the Ricker function from 12 to 50 % (Table 1; Eqs. 1b & 2c). There was no correlation or trend between $\mathrm{FIN}_{\mathrm{Feb}}$ and the respective environmental drivers, $\mathrm{HEL}_{\mathrm{Feb}}$, $\mathrm{CAL}_{\mathrm{Feb}}$ and $\mathrm{NAO}_{\mathrm{DJFM}}$. $\mathrm{HEL}_{\mathrm{Feb}}$ and $\mathrm{CAL}_{\mathrm{Feb}}$ were significantly, positively correlated
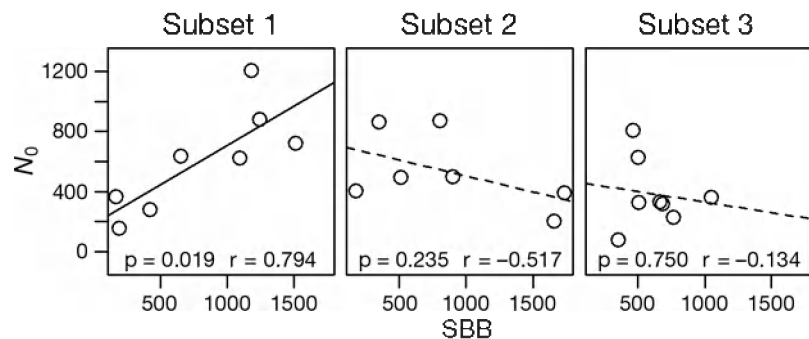

Fig. 1. *Ammodytes marinus*. Relationship between sandeel spawning stock biomass (SSB [10^3 t of age-2 and older]) and sandeel recruitment (N_0 [10^9 age-0 ind.]), under different scenarios of age-1 sandeel abundances (N_1 [10^9 age-1 ind.]). Data were disaggregated into 3 data subsets of equal sizes according to the age-1 abundance of the given year. Subset 1: <145 billion age-1 ind., Subset 2: between 145 and 275 billion age-1 ind. and Subset 3: >275 billion age-1 ind. The stock recruitment relationship in each subset was analysed using Pearson's correlation analysis with Spearman's test. Correlation coefficients (r) and p-values (p) are provided. A solid regression line is provided when the relationship is significant

Table 2. Including environmental drivers (FIN_{Feb}, HEL_{Feb}, CAL_{Feb} and NAO_{DJFM}) one-by-one in Eqs. (1a) & (2a) (see Table 1). The table shows the estimated coefficients for each environmental explanatory variable; p-values indicate whether the coefficients differed significantly from 0. ***p < 0.001

Model	Environmental driver	Coefficients	p
Eq. (1a)	FIN_{Feb}	225.00	<0.001***
Eq. (1a)	HEL_{Feb}	−16.57	0.625
Eq. (1a)	CAL_{Feb}	23.30	0.867
Eq. (1a)	NAO_{DJFM}	−5.13	0.447
Eq. (2a)	FIN_{Feb}	54.46	<0.001***
Eq. (2a)	HEL_{Feb}	0.01	0.748
Eq. (2a)	CAL_{Feb}	0.01	0.699
Eq. (2a)	NAO_{DJFM}	−1.30	0.463

(r = 0.94, p < 0.001), and CAL_{Feb} showed an insignificant negative trend with NAO_{DJFM} (r = 0.36, p = 0.088).

The importance of a species-specific *Calanus* index was explored more closely. In Fig. 2, the 3 *Calanus* indices are plotted together, with the residuals from a modification of Eq. (1b) (see Table 1) in which FIN_{Feb} was replaced by CAL_{Feb}. The plot illustrates that when a high *Calanus* spp. abundance is driven by HEL_{Feb}, it usually coincides with overestimation of recruitment. On the contrary, when HEL_{Feb} and FIN_{Feb} contribute equally to overall abundance, the model tends to underestimate recruitment.

In summary, these results support Hypothesis 2 by showing: (1) that only FIN_{Feb} was significantly related to N_0 and (2) that large overall *Calanus* abundances driven by *C. helgolandicus* were associated with medium to low N_0.

Model validation and selection

The last step in the analysis involved model selection according to AIC and r^2 and validation of the selected model using various methods. AIC was slightly lower for the final LM (Table 1; Eq. 1b) compared to the extended Ricker model (Table 1; Eq. 2c), and the final LM explained 65% of the inter-annual variation in N_0 compared to 50% in the extended Ricker function. Furthermore, it was regarded as a strength of the LM that, when fitted solely to population data (Table 1; Eq. 1a), the model could still explain as much as 30% of the variation compared to 12% in the Ricker model. Further model validation was therefore focused on the final LM (Table 1; Eq. 1b).

SSB showed a significant trend over time (p = 0.006), whereas there was no significant trend over time in the N_0, N_1, or FIN_{Feb} time series (p = 0.237, p = 0.379, p = 0.125, respectively). 'Year' was included in the final LM as a dummy variable to test for effects of linear trends over time, and the coefficient estimate was insignificant (p = 0.529). However, values dropped in all time series in 2002 and remained at a relatively low level for the rest of the study period. The final LM was therefore refitted to a subset in which data from 2002 and onward had been removed, and the new estimated coefficients were significant for all explanatory variables (SSB: p = 0.044; N_1: p = 0.043; FIN_{Feb}: p < 0.001; SSB–N_1 interaction: p = 0.006), which verified that the model was not driven by this drop.

Pairwise correlations of explanatory variables in the final LM showed no collinearity problems. Cook's distance analysis confirmed that the model was not influenced by single points driving the analysis. There was no autocorrelation in the model residuals, and they met the normality criteria (Kolmogorov-Smirnov test,
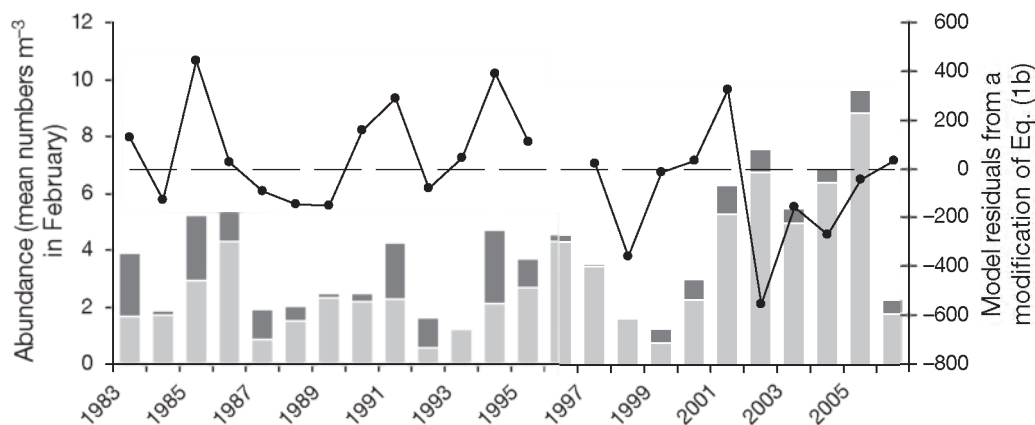

Fig. 2. Exploring the importance of a species-specific *Calanus* index. The histogram (left axis) is *C. finmarchicus* (dark grey columns) and *C. helgolandicus* (light grey columns). The line plot (right axis) shows model residuals from a modification of Eq. (1b) in which FIN_{Feb} was replaced by CAL_{Feb} (see Table 1). The horizontal dashed line is the boundary between negative and positive residuals (1996 is not plotted, see 'Materials and methods')

p = 0.126). Lastly, no trend was found in the model residuals versus the explanatory variables.

Fitted values from the final LM and observed N_0 values showed a high degree of covariation (for a dataset without 1996: r = 0.806, p < 0.001; Fig. 3A). Mean prediction error in the bootstrap-based cross validation was 0.582, with 24.5% of 1000 iterations resulting in coefficients <0.5 (Fig. 3B). The year 2002 was the only year (other than 1996) that completely departed from the pattern predicted by the model. If 2002 was left out during cross validation, the mean prediction error was considerably reduced, leading to an increase in the mean correlation coefficient from 0.582 to 0.780. Furthermore, only 3.2% of 1000 iterations then resulted in coefficients <0.5 (Fig. 3C). The cross validation mean prediction error was slightly increased when the LM was trained mainly on years before 2000 (Fig. 3D)

The results of the model validation suggested that a linear model based on FIN_{Feb} and interactions between N_1 and SSB (Table 1; Eq. 1b) provides the most accurate and precise description of N_0 and that the predictive capability of such a model is rather high, considering the available time series.

DISCUSSION

Density dependence

The results of the present study support the findings by Arnott & Ruxton (2002) that lesser sandeel *Ammodytes marinus* recruitment in the North Sea is under density-dependent regulation, mainly driven by the age-1 population. However, the present results additionally show how a positive relationship between spawning stock biomass (SSB) and recruitment (N_0) was decoupled in years associated with a large age-1 population (N_1). Consequently, inclusion of the interaction (non-additive effect) between SSB and N_1 was necessary in order to model recruitment. When SSB–N_1 interactions were included in the linear model, around 30% of the inter-annual variation in N_0 could be explained. In comparison, a traditional Ricker function explained no more than 12% of the variability in the recruitment. This result strongly suggests that the lesser sandeel population of the North Sea, between 1983 and 2006, made a shift between a state below carrying capacity, where the classical spawning stock–recruitment relationship prevailed, and a state above carrying capacity, where state-dependence mediated by the age-1 population prevailed. In turn, this also explains why a simple additive (without interactions) spawning stock–recruitment relationship and a traditional Ricker function perform poorly (Arnott & Ruxton 2002, ICES 2007, present paper).

A traditional Ricker function (Ricker 1954) has inherent density-dependent assumptions and models a positive spawning stock–recruitment relationship at a low spawning stock biomass and a negative relationship at a high spawning stock biomass. Furthermore, it does not take age-1 abundance into account. Since the age-1 population in most years by far outnumbers the spawning stock (ICES 2007), it is not surprising that density dependence is mediated mainly by age-1 abundance.
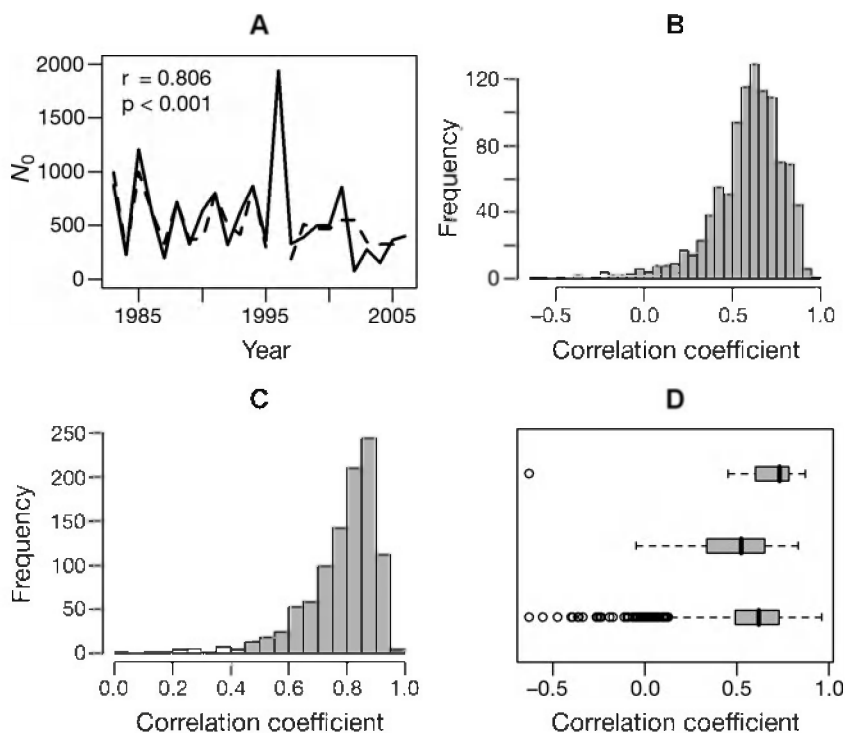

Fig. 3. Validating the linear regression modelling (Table 1; Eq. 1b). (A) Covariation plot of fitted values (broken line) versus observed values (solid lines). Note: the unusually high N_0 of 1996 was neither included in the model fitting nor in the covariation analysis. Pearson's correlation coefficient and p-value (Spearman's test) were calculated after removing 1996 data. (B) Distribution of prediction errors (Pearson's correlation coefficient) from bootstrap-based cross validation. (C) As for (B) but removing 2002 data. (D) Boxplot comparing the total distribution of prediction errors from the cross validation (lower box) to subsets of the prediction errors. Subset 1 is where only 1 yr after 1999 was included in the data subset used to train the model (middle box). Subset 2 is where only 1 yr before 1990 was included (upper box)

The Ricker function, therefore, is an inadequate way to account for density dependence in a sandeel population. It should be noted that an attempt to include total population biomass or number was made. The attempt was unsuccessful, since these measures are related to SSB and causes collinearity among explanatory variables.

Cannibalism on eggs and larvae are common causes of density dependence. Lesser sandeels spawn in December/January, and the eggs stick to the substrate until they hatch during February and March (Wright & Bailey 1996). Intra-specific predation on eggs and larvae by lesser sandeels may be insignificant, since the majority of lesser sandeels presumably reside passively in the sediment all winter (Reeves 1994), although a few fish may leave the sediment during winter, also outside the spawning period (Høines & Bergstad 2001). Furthermore, its close relative, *Ammodytes tobianus*, seems incapable of bottom-feeding (M. van Deurs pers. obs.). Lesser sandeels generally forage between April and June, when zooplankton is most abundant (Winslade 1974c). By this time most larvae are >20 mm and highly mobile (Wright & Bailey 1996, Jensen et al. 2003). Therefore, they are highly unlikely to represent a significant food source for age-1 sandeels.

Another source of density dependence is competition for food resources. If the high concentrations of age-1 sandeels occurring in some years deplete food resources locally, newly metamorphosed sandeels would experience reduced growth. Biro et al. (2003) showed how density-dependent competition for food promotes risk-taking behaviour in age-0 rainbow trout *Onchorhynchus mykiss* as a strategy to counteract reduced energy uptake and thereby minimize the expected risk of overwinter starvation. In the case of age-0 sandeels, reduced growth could potentially force young sandeels to either prolong their feeding period and postpone the submerged low risk overwintering stage or to feed in more risky habitats further away from their sand refuge. Both scenarios would lead to increased predation mortality. The idea that young sandeels may be forced to postpone overwintering in years of poor growth conditions is consistent with observations of large quantities of age-0 individuals in the pelagic in September (Winslade 1974a, Reeves 1994).

Species-specific *Calanus* abundance and the NAO

The present study provides empirical documentation that sandeel recruitment in the North Sea is positively correlated to *C. finmarchicus* (Stages V and VI) abundance in February. In contrast, overall *Calanus* spp. or

C. helgolandicus abundance was not significantly correlated to recruitment. This is contrary to findings by Arnott & Ruxton (2002), who found overall *Calanus* spp. abundance in February to be associated with North Sea sandeel recruitment. However, their time series extended from 1983 to 1999, and the species specificity observed in the present study was particularly pronounced after 1999, when a dramatic *C. helgolandicus*-driven increase in overall *Calanus* spp. abundance coincided with years of poor sandeel recruitment. The significance of the situation in recent years was also reflected in the model validation, which suggested that a full description of the covariate space was only possible if recent years were included when training the model.

In the North Sea, *Calanus finmarchicus* and *C. helgolandicus* are of equal size. Unfortunately, a comparison of female lipid content is not available. It is, however, known that both location and timing of egg production differs in these species (Jónasdóttir et al. 2005). A mismatch between the timing of prey availability and critical sandeel larval stages, therefore, provides the best explanation for the results presented here.

Dependence on a particular zooplankton species has been well documented for herring *Clupea harengus*, for example a decline in *Pseudocalanus* sp. abundance coincided with a 50 to 60 % reduction in the mean weight at age for Baltic herring between 1980 and 1997 (Cardinale & Arrhenius 2000, Möllmann et al. 2005). Furthermore, the horizontal distribution of North Sea herring during summer foraging changed according to a climate-driven shift in *Calanus finmarchicus* distribution (Corten 2000).

Horizontal distributions of *Calanus finmarchicus* and *C. helgolandicus* overlap in the North Sea, where their biogeographical boundaries meet (Planque & Fromentin 1996). They display dissimilarities with respect to life cycles and temperature optimums, and climate has a significant influence on the horizontal distribution and regional species composition of these copepods (Fromentin & Planque 1996, Heath et al. 1999, Beaugrand 2003). *C. finmarchicus* prefer deeper and colder water compared to *C. helgolandicus* and do not overwinter in the North Sea but off the shelf in deep Atlantic water. The overwintering stock of *C. finmarchicus* in the Faroe–Shetland Channel ascends to the surface, starting in February, with a peak in March and April, when north-westerly winds transport Stage V (CVs) and females into the North Sea (Heath 1999, Heath et al. 1999).

Since spatial and temporal variation in *Calanus* spp. composition and abundance is climate driven, it would be expected that the NAO at least indirectly affects sandeel recruitment. However, in the present

study NAO_{DJFM} was not found to covary with CPR measures of *C. finmarchicus*, but only with *C. helgolandicus* and overall *Calanus* spp. abundance. Heath et al. (1999) found that the inflow of *C. finmarchicus* from the Atlantic was influenced by the NAO, but the effect was only evident on decadal timescales and not from year to year, which could explain why the NAO, as a proxy for climate conditions, was not found to be associated with sandeel recruitment in the present study.

Does the model overlook something?

Model validation documented the reliability and predictive capabilities of the final linear model (Table 1; Eq. 1b). However, only when model fitting was carried out without 1996 did the resulting model emerge. The year 1996 was a climatic extreme associated with a dramatic shift in slope water circulation patterns in the NW Atlantic (Greene & Pershing 2003), and coincided with an unusually large recruitment of lesser sandeels (Frederiksen et al. 2006, ICES 2007). Except for the concurrence of the highest recruitment and the lowest NAO_{DJFM} in 1996, the NAO index applied in the present study did not contribute to the recruitment model. The link between the climatic phenomenon of 1996 and sandeel recruitment therefore remains unknown.

The year 2002 also deserves special attention. Predictive performance of the final LM was particularly high when 2002 was excluded. The spatial overlap between herring and sandeel in 2002 was, according to the catches from the Quarter 1 'International Bottom Trawl Survey' (data available from http://datras.ices.dk/Home/Access.aspx, accessed May 2005), the largest of the entire time series analyzed in the present study (M. van Deurs unpubl. data). It has been suggested that herring influence sandeel recruitment in the Shetland population (Frederiksen et al. 2007), and sandeel larvae are often found in herring stomachs (Savage 1937, Pommeranz 1981, Last 1989). Hence, poor fit of the model in 2002 may be a consequence of unusually high predation pressure exerted by herring.

The analyses presented here target the entire stock located in ICES Division IVb east of 0° E, also referred to as the North Sea sandeel. It has often been suggested that this stock should be regarded as a metapopulation consisting of a number of subpopulations separated by distance and the physical oceanography (e.g. Pedersen et al. 1999, Arnott & Ruxton 2002). The sandeel populations along the east coast of Scotland and the Shetland Islands are already managed separately from the North Sea sandeel. However, we found that the scientific foundation for subdividing the North Sea sandeel into sub-components is still not solid enough to be applied. Furthermore, the long CPR time series and the population assessment data cannot support a spatially explicit analysis. The North Sea sandeel is found on most offshore sand banks in ICES Division IVb, but landings indicate that the Dogger area is quantitatively the most important area (ICES 2007). This area therefore largely drives the stock assessment from which the population data used in the present study were taken. The Dogger area has also experienced relatively good CPR coverage, and a CPR index for *Calanus finmarchicus* calculated for the Dogger area alone is highly correlated with that of the entire ICES Division IVb (c = 0.855, p < 0.001). It is therefore likely that the model proposed in the present study represents the sandeels populating the Dogger area rather than the more peripheral stock components.

Perspectives

The results of the present study provide an example of: (1) how models that account for density dependence should be specifically adapted to match the biology of the individual population and (2) how climate change may affect population dynamics indirectly by altering prey species composition.

During the last decade, regional *Calanus* species composition within the North Sea has changed significantly as a result of recent climate changes (Beaugrand 2003). Predictions indicate that these changes will persist or even increase (Pachauri & Reisinger 2007). A large sandeel fishery has been exploiting the sandeel stock in the North Sea for decades, apparently without causing the stock to decline. The fishery mainly exploits the spawning stock biomass, which may not affect recruitment in stocks that are subjected to density-dependent regulation until the stock is below a critical limit. However, as shown in the present study, climatic forcing could potentially reduce the carrying capacity as it modifies the food resource and thereby forces the stock size below this critical limit. When the stock falls below the critical limit the spawning stock–recruitment relationship becomes important, and fishing mortality is now likely to indirectly affect recruitment by reducing the spawning stock. Depleted stocks are more vulnerable to changes in the environment (Brander 2005) and are therefore much more likely to crash. A decline in the North Sea sandeel stock will affect up to 10 species of predatory fishes (Engelhard et al. 2008), as well as a number of bird species and marine mammals (Furness 1990, Hain et al. 1995, Furness 2002, Frederiksen et al. 2005).

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