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Temperature and body size affect recruitment and survival of sandeel across the North Sea

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Climate effects on marine fish depend on life stage, particularly when life stages differ in habitat utilization. In the present study, we investigated life stage-dependent responses of lesser sandeel (*Ammodytes marinus*) to temperature at contrasting geographical scales. We related population density and individual growth to temperature and found different temperature responses between the first and the second years of life. During the first year of life, fish size was the single most important factor influencing sandeel abundances, indicating a positive relationship between growth and survival. In contrast, during the second year of life, autumn bottom temperature was negatively correlated with sandeel abundance, suggesting elevated mortality in warm years. Southerly areas, experiencing higher temperatures in general, were also the areas showing the strongest response to temperature. This study sheds light on how warming impacts population dynamics of one of the most important forage fishes in the North Sea and supports the discussion of underlying mechanisms.

Keywords: *Ammodytes*, climate change, forage fish, length, life history, ontogeny, productivity, recruitment, short-lived species, warming

Introduction

Climate change and climate variation is affecting the distribution and productivity of a variety of marine organisms, including fish (Brander, 2007; Brierley and Kingsford, 2009; Hollowed *et al.*, 2013). Reliable predictions of these changes provide the necessary foundation for understanding which adaptation strategies provide the most desirable future for both fish stocks and fisheries. However, studies have demonstrated that the observed responses to changes in temperature depend on the life phase considered (e.g. Gillooly *et al.*, 2002; Barbeaux and Hollowed, 2018) and the spatial resolution of the study (Tuya *et al.*, 2011; Ciannelli *et al.*, 2012). The same species may even show contrasting responses across life stages due to differences in ecology (Pörtner and Peck, 2010; Petitgas *et al.*, 2013). Such differences can lead to opposing predictions of stock development under climate change scenarios. Properly considering multiple life stages at different scales is therefore key to the climate adaptation of fisheries management.

The lesser sandeel (also Raitt's sandeel, *Ammodytes marinus*) is one of the most abundant forage fish species in the North Sea and is considered as an essential part of the mid-trophic level in the ecosystem (Furness, 2002). Behaviour, life history and geographical distribution within the North Sea are thoroughly described in the scientific literature (e.g. Macer, 1966; Winslade, 1974a, b, c; Wright and Bailey, 1996; van Deurs *et al.*, 2010) and research has demonstrated the effect of temperature (e.g. linked to climate change) on productivity and survival of early life stages (i.e. indicated by the recruitment) (e.g. Arnott and Ruxton, 2002; van Deurs *et al.*, 2009; Lindegren *et al.*, 2018). However, the effect of temperature later in life remains largely unresolved. Furthermore, studies that have reported temperature–recruitment correlations are mainly conducted at the regional scale (i.e. the central or western North Sea) using data with little or no spatial resolution.

The life cycle of lesser sandeel (hereafter just "sandeel") includes distinct phases. Sandeel hatch from eggs attached to sand grains and begin a short larval drift phase before developing active swimming and juvenile schooling behaviour (Potter and Lough, 1987; Proctor *et al.*, 1998). After metamorphoses at a length of c. 40–50 mm, they settle into a patchwork of sandy habitats in the North Sea in early summer, joining the adult segment of the population (Christensen *et al.*, 2007, 2008, 2009). After settling, they immediately adopt adult behaviour that includes nocturnal burying and high site fidelity (Wright *et al.*, 2000, 2019; Holland *et al.*, 2005). Maturation occurs around the ages of 1–3 (Boulcott *et al.*, 2007). The annual cycle of settled juveniles and adults is divided into feeding and overwintering phases. During overwintering, the fish bury in the sand, surviving on energy reserves (van Deurs *et al.*, 2011b). The overwintering extends from late summer, interrupted only by spawning in January (Gauld and Hutcheon, 1990). Juveniles may postpone burying for a couple of months to gain additional resource storage (Reeves, 1994; van Deurs *et al.*, 2010, 2011a). During spring, they emerge again from the sand to forage during the day and bury in the sediment at night (Winslade, 1974c; Freeman *et al.*, 2004).

Sandeel productivity in the North Sea is possibly affected by temperature during multiple life stages. Gonad investment is inhibited at high winter temperatures (Wright et al., 2017a, b) while spawned demersal eggs develop faster (Régnier *et al.*, 2018), resulting in fewer eggs, earlier hatching, and smaller sizes of the hatching larvae. The pelagic larvae are assumed to drift passively with the prevailing current (Berntsen *et al.*, 1994; Christensen

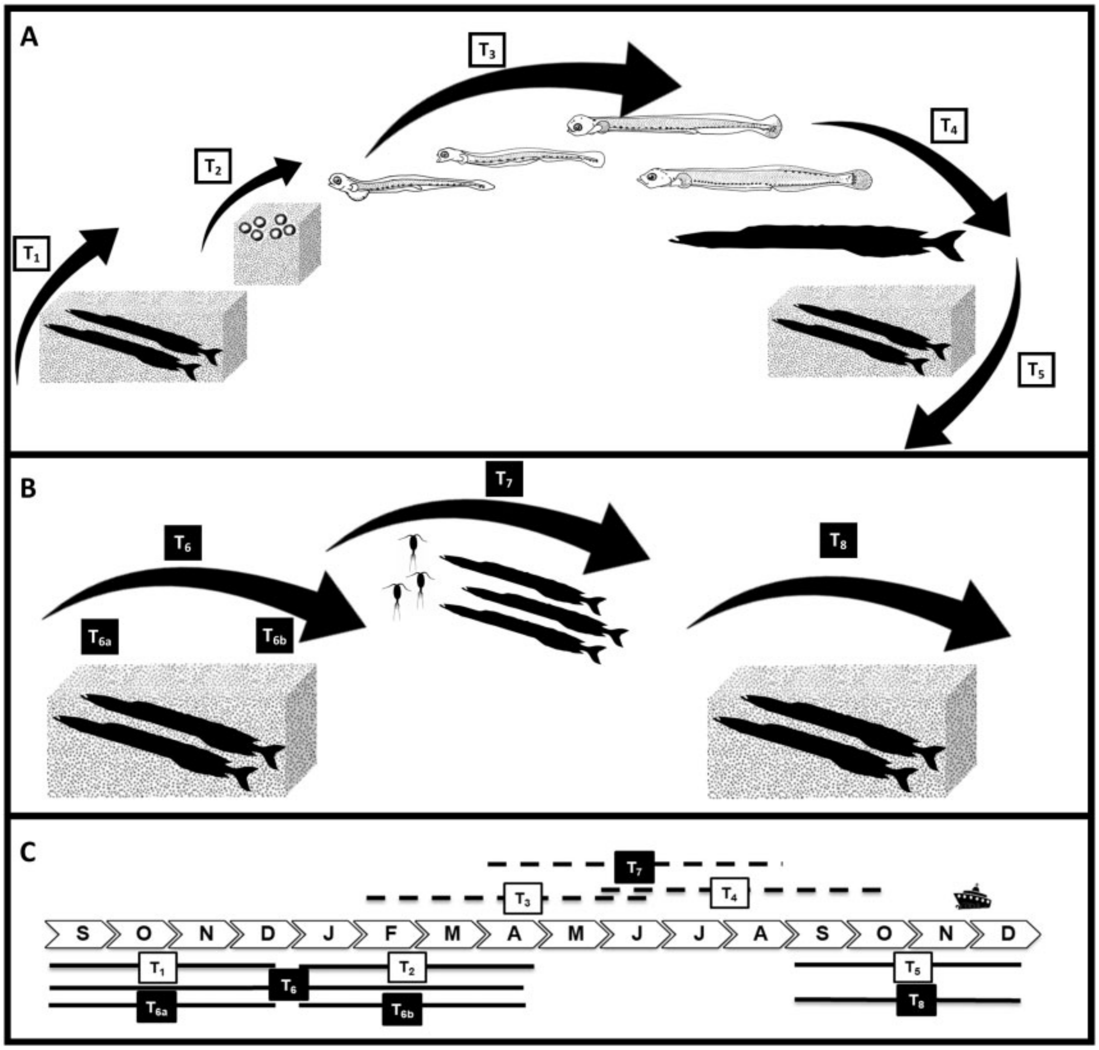

Figure 1. Schematic representation of hypotheses of how different temperatures relate to different phases of the sandeel life cycle. (A) Five different phases during the first year of life (age-0) illustrated by pictograms connected by arrows, starting with mature sandeel prior to spawning (i.e. egg developing in gonads), then the egg phase, larval phase, and metamorphosis, and finally ending with the first half of the first overwintering period. Temperature hypotheses are illustrated by black boxes (T_1 to T_5). (B) Three phases of the second year of life (age-1) illustrated by pictograms connected by arrows, starting with the second half of the first overwintering period, followed by a feeding period, and ending with the first half of the second overwintering period. Temperature hypotheses are illustrated by white boxes (T_6 to T_8). (C) Illustration of how each temperature hypothesis (reusing the boxes in A and B) uses an average temperature, covering four or more months. Months are illustrated by arrow boxes with the first letter of each month inside. The extent and position of horizontal lines shows which months are used for the respective average temperatures. Sea surface temperature is represented by dashed lines and bottom temperature by solid lines. The timing of the Danish sandeel survey is illustrated by ship pictograms.

Table 1. Detailed summary of the different temperature hypotheses.

Age group	Temperature abbreviation	Expected effect direction	Temperature and life phase	Reported effects	References
0	T_1	Negative	SBT experienced by parents prior to spawning	Warming inhibit gonad development in adults Ovarian development delayed	Gauld and Hutcheon (1990) and Wright *et al.* (2017a, b)
0	T_2	Positive /negative	SBT during egg incubation and hatching	Egg development rate increases with warming Indirect effects of temperature causing mismatch between larvae and zooplankton	Régnier *et al.* (2018, 2019)
0	T_3	Positive	SST during the larval drifting phase	Larval growth rates are higher in warm waters	Christensen *et al.*(2008)
0	T_4	Positive /negative	SST during the post-settlement foraging	Higher temperatures increase metabolism and digestion rate and therefore growth potential, but only if sufficient amount of food is available. Otherwise, higher temperature will lead to diminished growth and potentially reduced survival	van Deurs *et al.* (2014, 2015)
0	T_5	Negative	SBT during the first months of juvenile overwintering until the sandeel survey takes place	Warming has a negative impact on overwintering	van Deurs *et al.* (2011b) and MacDonald *et al.* (2018)
1	T_6	Negative	SBT during the full overwintering period	Warming has a negative impact on overwintering	van Deurs *et al.* (2011b) and MacDonald *et al.* (2018)
1	T_{6a}	Negative	SBT during the first half of the overwintering period	Warming has a negative impact on overwintering	van Deurs *et al.* (2011b) and MacDonald *et al.* (2018)
1	T_{6b}	Negative	SBT during the second half of the overwintering period	Warming has a negative impact on overwintering	van Deurs *et al.* (2011b) and MacDonald *et al.* (2018)
1	T_7	Positive /negative	SST during the annual foraging window starting in spring	Higher temperatures increase metabolism and digestion rate and therefore growth potential, but only if sufficient amount of food is available. Otherwise, higher temperature will lead to diminished growth and potentially reduced survival	Winslade, (1974b) and van Deurs *et al.* (2014, 2015)
1	T_8	Negative	SBT during the first months of the adult overwintering period until the sandeel survey takes place	Warming has a negative impact on overwintering	van Deurs *et al.* (2011b) and MacDonald *et al.* (2018)

et al., 2007, 2008) while the temperature of the surrounding water determines growth and survival (Gurkan *et al.*, 2012, 2013). After settlement, temperature may influence growth conditions (Rindorf *et al.*, 2016), which in turn determine the timing of the onset of overwintering. When overwintering has begun, bottom temperature determines the rate at which energy reserves are expended (van Deurs *et al.*, 2011b).

In the present study, we examined which phases of the sandeel life cycle population dynamics are influenced by changes in temperature. We used statistical models to test a sequence of temperature hypotheses (Figure 1 and Table 1) divided into recruits and young adults by age-structured abundance indices calculated for nine distinct subareas (Figure 2a). Abundance indices were derived from a scientific sandeel survey, and while the International Council for the Exploration of the Seas (ICES) uses the survey for stock assessments, it is used here for the first time in a research context. Our main research questions were threefold: (i) how does temperature affect important phases of the life cycle of sandeel, (ii) what is the importance of temperature compared to other factors, such as density dependence and body size, and (iii) does the effect of temperature change on a spatial scale.

Material and methods

Survey data

Denmark initiated a survey programme in 2004 to estimate recruitment for the ICES sandeel stock assessments (ICES, 2010). The survey uses a modified scallop dredge to measure the abundance of sandeel in the seabed during night-time in late November or early December. The survey covers most of the sandeel habitat in the North Sea and uses a fixed station design, even though the surveyed area has gradually expanded over time and therefore new stations have been added. At each fixed survey station, three 10-min hauls are conducted in a way so that each haul intercepts the position about half way and with an angle to the other hauls (i.e. ideally the three hauls form a star). Samples are

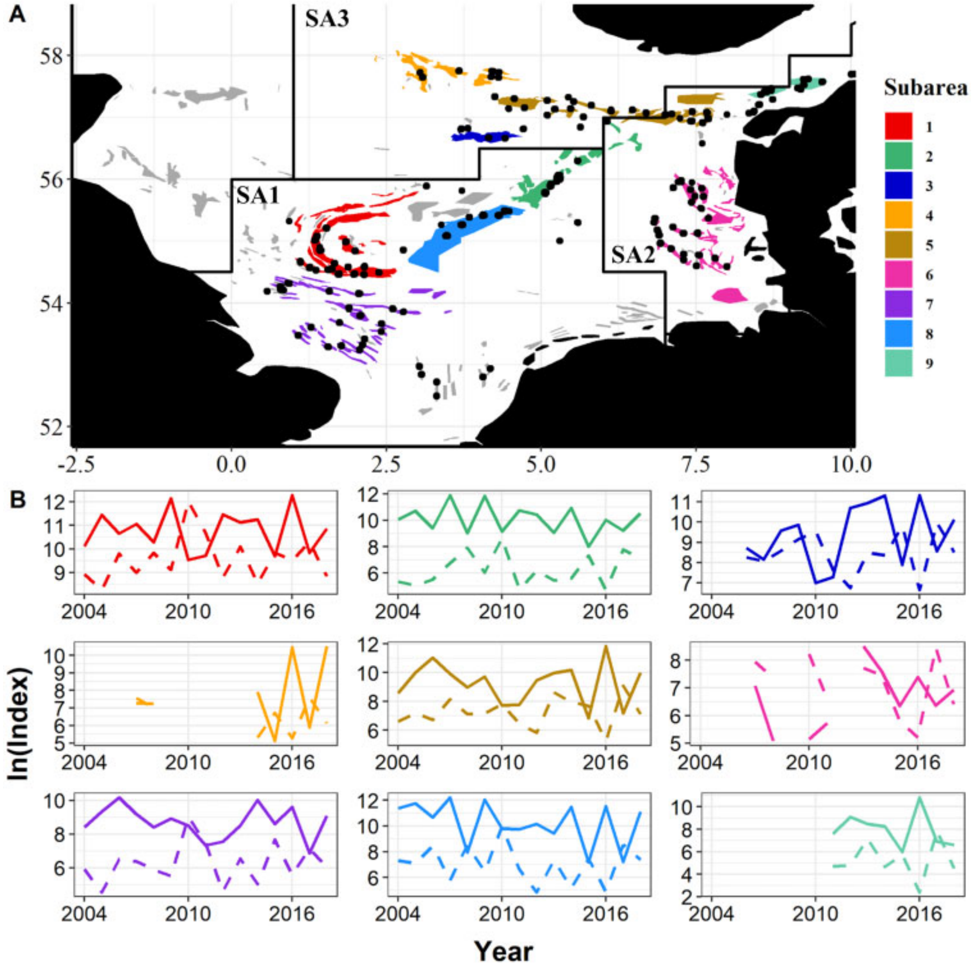

Figure 2. (A) Map of sandeel habitat (polygons) and survey stations (black dots). The colour coding of the polygons represents the nine subareas used in the study. Sandeel habitat not used in the present study is shown in grey shading. ICES sandeel management areas SA1, SA2, and SA3 are superimposed on top of the subareas. (B) Time series of log-transformed abundance indices produced from survey data for age-0 (solid lines) and age-1 (dashed lines). Differences in time-series lengths are due to the survey being expanded (geographically) in 2006, 2011, and 2014. Missing years are due to insufficient data to produce reliable age-length keys (see description in Material and Methods).

weighed and all fish are counted and measured (total length rounded down to the nearest half-centimetre). Ten sandeel from each half-centimetre length-class (or all if fewer than 10 are available) are weighed (in grams with two decimals) and aged based on the number of otolith winter-rings. In case of very large catches, a sub-sample is weighed and counted, and the total number of sandeel is estimated by scaling up to the weight of the total sample.

Abundance indices

Annual abundance indices were calculated for each of nine subareas and for age-0 and age-1, separately (Figure 2). Subareas were adopted directly from ICES (2016) and are constructed by combining patches of sandeel habitat (described in Jensen *et al.*, 2011). Note that time-series length varies between subareas, as the surveyed area was expanded over years, but consistency of the area coverage has been relatively stable throughout the survey (Figure 2a). A delta-lognormal model was applied to numbers at age by haul. To obtain age-structured haul data, smooth age-length keys (ALKs) were estimated for all combinations of year and subarea, respectively (Berg and Kristensen, 2012), and numbers at age by haul were then calculated by combining the observed numbers at length by haul and the ALKs. Year-subarea combinations, where the ALK was based on <10 fish, were excluded from subsequent analyses. The delta-lognormal model is a combination of a binomial presence/absence model and a lognormal model for strictly positive numbers (Pennington, 1983; Berg *et al.*, 2014) and included year and subarea as explanatory variables. The approach is similar to how ICES calculate the sandeel survey indices for the assessment models (see Supplementary materials for more details). The index for age-0 fish was regarded as a measure of the number of recruits (i.e. recruitment) and the age-1 index represented the abundance of young adults entering the second winter of their life.

Growth indices

Growth was analysed using two indicators, length and condition factor, reflecting long-term and medium-term balance between feeding and metabolism, respectively. Length at age (cm) was calculated by year and subarea using the ALKs mentioned in the

Table 2. Summary statistics from the final mixed effects models for age-0 and age-1 after model selection.

Model	**Final model**	**$R^2{}_m/R^2{}_c$**	***n***
Age 0	$ln\,\hat{I}_{0,i,y} \sim gL_{0,i,y} + \acute{\varepsilon}_i + \acute{\omega}_{y,m}$	0.08/0.72	101
Age 1	$ln\,\hat{I}_{0,i,y} \sim kT_{8,i,y} + nlnI_{0,i,y-1} + \acute{\varepsilon}_i + \acute{\omega}_{y,m}$	0.44/0.84	81

	Parameter	**Estimate**	***p*-Value**	***SD***	**Groups**
Age 0	Length effect (*g*)	0.398 (0.140)	0.004**		
	Random effect of subarea ($\acute{\varepsilon}_i$)			0.988	9
	Random effect of year:management area ($\acute{\omega}_{y,m}$)			0.857	38
	Residual error			0.853	
Age 1	Temperature effect (*k*)	−0.417 (0.144)	0.003**		
	Recruitment effect (*g*)	0.463 (0.086)	<0.001***		
	Random effect of subarea ($\acute{\varepsilon}_i$)			0.825	9
	Random effect of year:management area ($\acute{\omega}_{y,m}$)			0.509	38
	Residual error			0.600	

The dependent variables were logarithm-transformed (ln) abundance indices for age-0 (I_0) and age-1 (I_1). The best age-0 model included only fish length (L). The best age-1 model included temperature during the early overwintering period (T_8) and recruitment in the preceding year ($\ln I_{0,y-1}$). Numbers in parentheses are SE for estimates of fixed effect coefficients and SD for random effects. Also, the variance explained for fixed effects ($R^2{}_m$), combined fixed and random effects ($R^2{}_c$), and the *p*-values (Wald Z-statistics) are presented.

*$p < 0.05$,

**$p < 0.01$,

***$p < 0.001$.

section above. Weight at age (g) was calculated based on a length–weight relationship (power function) fitted to the observed lengths and weights for each combination of age, year, and subarea. Condition factor at a given age was estimated as $C = W/L^b$, where W is the weight at age, L is the length at age, and b is 3.06 (adopted from van Deurs *et al.*, 2013).

Temperature indices

Estimates of sea bottom temperature (SBT) and sea surface temperature (SST) for all years (2003–2018) were obtained from the North-West European Shelf-Ocean Physics Reanalysis from MetOffice issued under the European Commission (Copernicus website: http://marine.copernicus.eu/). The dataset offers daily temperature estimates across a grid consisting of longitudinal–latitudinal 7 km^2 cells. To achieve subarea-specific estimates of SBT and SST, temperature estimates were averaged across grid cells overlapping the geographical extent of the subareas (Figure 2a). Besides the spatial dimension of temperature, the temporal dimension were considered by averaging across critical time windows, following recommendations from van de Pol *et al.* (2016). In total, ten different average temperatures (SBT or SST), covering eight different life phases, were calculated. The expectation was that one or more of the first five temperatures influence the abundance of age-0 sandeel, whereas, one or more of the remaining five temperatures influence the abundance of age-1 sandeel (Table 1 and Figure 1).

Effects of temperature, population size and growth

Linear mixed models (LMMs) were used to test if spatio-temporal variation in water temperature was significantly related to variation in the abundance of age-0 and age-1 sandeel. The time series of abundance indices obtained from the survey constituted the dependent variables, and the time series of temperature constituted the independent variables. The ten different temperatures were tested one at a time in separate models. Abundance of age-0 (i.e. recruitment) and age-1 (i.e. young adults) was also treated in separate models with slightly different model formulations to match the hypotheses stated in Table 1.

There are three ways in which the abundance of sandeel in any given year may impact abundance in the subsequent year. First, a large proportion of the age-1 sandeel caught in the survey (in November/December) contributes to the spawning stock biomass on 1 January. In most years, age-1 sandeel constitute the bulk of the spawning stock biomass (ICES, 2016); hence, the abundance of age-1 sandeel may therefore have a positive effect on the abundance of age-0 sandeel in the following year. Second, previous studies have indicated that sandeel recruitment is negatively correlated to the number of age-1 sandeel in the stock, presumably due to cannibalistic behaviour and resource competition (van Deurs *et al.*, 2009; Eigaard *et al.*, 2014). Hence, the age-1 index was not only used as the dependent variable in the age-1 models but also used as an independent variable in the age-0 models as an indicator of the size of the local spawning stock proxy (with a one year lag) and as a measure of local density dependence (with zero year lag). Lastly, abundance of age-1 fish is highly dependent on the recruitment in the preceding year (Rindorf *et al.*, 2019). Hence, the age-1 model included the age-0 index (with a one year lag) to account for year-class strength. Both the age-0 models and the age-1 models included length at age to account for the potential effect of growth on for example survival. Moreover, condition factor at age was included in models to differentiate between growth conditions experienced in the previous year and growth conditions experienced in the current year.

The LMM formulations can be summarized as follows for age-0 and age-1, respectively:

$$\ln \hat{I}_{0,i,y} \sim b + cT_{p,i,y} + d\ln I_{1,i,y} + f\ln I_{1,i,y-1} + gL_{0,i,y} + hC_{0,i,y} + \varepsilon_i + \omega_{y,m},$$

$$\ln \hat{I}_{1,i,y} \sim j + kT_{p,i,y} + n\ln I_{0,i,y-1} + oL_{1,i,y} + rC_{1,i,y} + \varepsilon_i + \omega_{y,m},$$

where *b*, *c*, *d*, *f*, *g*, *h*, *j*, *k*, *n*, *o*, and *r* are parameters to be estimated, $I_{a,i,y}$ is the logarithm-transformed (ln) abundance index for a given age (a), subarea (i), and year (y), $T_{p,i,y}$ is the average temperature during a given life phase (p), subarea, and year, $L_{a,i,y}$ and $C_{a,i,y}$ are the average length and condition factor at a given age, subarea, and year. Random effects of subarea, $\acute{\varepsilon}_i \sim N(0, \sigma^2_{\acute{\varepsilon}})$, and year on the intercept were included in both models. However, since the year effect was assumed not to be constant across all nine subareas, the random year effect, $\acute{\omega}_{y,m} \sim N\left(0, \sigma^2_{\acute{\omega}}\right)$, was modelled as an interaction term with management area (m) (see management areas in Figure 2a). Since five different temperature hypotheses were tested for each age group, each of the models described above were fitted five times, each time using a different temperature (see Table 1 and Figure 1). Note that two-way interactions (e.g. $T_1{:}T_2$, also see Supplementary Figures S9 and S10 for correlation between T's) between periods of temperature for each age group were included in initial models but were always reduced out in model selection.

Model selection was performed by comparing all models using AIC$_c$ (Hurvich and Tsai, 1989, 1995). If competing models obtained similar scores, i.e. ΔAICc < 2 (Burnham and Anderson, 1998), then the simplest model with only significant predictors ($p < 0.05$, Wald Z-statistics) was chosen as the final model. However, even if temperature was not part of the simplest model, it was re-introduced to the final model to obtain information about the slope estimate (i.e. age-0, Supplementary Table S2). Moreover, to investigate the effect of having shorter periods over long designated periods (i.e. assigned by life phase) of temperature, models that included monthly averages of both SBT and SST were investigated (Supplementary Figure S8). To investigate if local differences in the response to temperature existed between subareas, the final model was re-fitted to data from each subarea one by one (leaving out the random effect of subarea).

All models were fitted in R using glmmTMB (Brooks *et al.*, 2017). AIC$_c$, marginal and conditional coefficients R^2_m and R^2_c (Nakagawa and Schielzeth, 2013; Nakagawa *et al.*, 2017), and one-step-ahead prediction residuals (Thygesen *et al.*, 2017) were calculated and used as model diagnostics.

Results

Abundance indices

In all nine subareas, abundance indices fluctuated by a factor of c. 10 (i.e. the actual abundance index and not the logarithm transformed) between years (Figure 2). Year-to-year dynamics differed notably between subareas, except for age-0 abundance in 2009 and 2016, which was above average in all subareas. The quality (i.e. ability of the survey to follow cohorts) of the survey showed high internal consistency (i.e. the logarithm-transformed age-1 index in the current year as a function of the logarithm-transformed age-0 index in the preceding year) varying between 15% and 65% explained variance (>40% in five out of nine subareas) (see Supplementary Figure S1).

Effects of temperature, population size, and growth

After model reduction, the final model for age-0 abundance included the positive effect of fish length as the only significant predictor ($p < 0.004$, Wald Z-statistics) (see Supplementary Table S1 and Supplementary Figures S2 and S3 for more details about model selection and model fits). The variance explained by fixed effects and combined fixed and random effects was 8 and 72%, respectively (Table 2). The relationship between age-0 abundance and fish length was positive in eight subareas and significant ($p < 0.05$) in four out of nine subareas (see Supplementary Figure S4). No significant correlation between abundance and any of the tested temperature indices was seen in any subarea (see Supplementary Figure S5). Considering temperature over shorter periods of monthly averages did not change the overall conclusions (Supplementary Figure S8). Two-way interactions between periods of temperature were also considered but were always reduced out in the model.

After model reduction, the final model of age-1 abundance retained recruitment in the preceding year (i.e. I_0) ($p < 0.001$) and bottom temperature in late summer and autumn (i.e. T_8), the first part of the overwintering period ($p < 0.003$) (see Supplementary Table S1 and Supplementary Figures S3 and S6 for more details about model selection and model fits). The effect of temperature was negative, and the effect of recruitment in the preceding year was positive (Figure 3). The fixed effects explained 44% of the variance and the combined fixed and random effects explained 84% (Table 2). An additional analysis that looked at the effect of monthly temperatures supported the finding that T_8 represented the time period during which temperature exerts the strongest effect (Supplementary Figure S8).

Geographical differences in the effect of temperature

Fitting the final best model formulation to each subarea showed that the abundance of age-1 sandeel was positively related to recruitment in the preceding year (i.e. positive slope coefficients) in all nine subareas (significant slopes in five subareas) and negatively affected by temperature (T_8) in eight out of nine subareas (significantly negative slope in four subareas) (Table 3 and Figure 4a and b). A highly significant negative relationship ($p < 0.001$, explained variance = 87%) (Figure 4d) was apparent when the subarea-specific slopes of the temperature effects (from subareas with at least 7 years of survey data, see Figure 2b) were related to the average temperature of the respective subareas (averaged across all years). Geographically, the North Sea could roughly be divided into a northerly offshore cold area consisting of subareas exposed to average temperatures <10.5°C and a southerly and coastal area, consisting of subareas exposed to average temperatures >10.5°C (Figure 4c). The estimated slope coefficients were in general more negative (i.e. stronger temperature effect) in the warmer area (Figure 4a). Since none of the temperatures (T_1 to T_5) contributed significantly to the age-0 model, the results obtained from fitting a model that included temperature (Supplementary Figure S3) to each subarea, are only presented in Supplementary Table S2.

Discussion

The influence of temperature on sandeel abundance differed between the first year of life and the second year of life. During the first year of life, no relationship with temperature was found for any of the five temperatures tested. In contrast, during the second year of life, the change in abundance of age-1 was significantly related to bottom temperature at the beginning of the overwintering period (T_8), and southerly areas experiencing higher average temperatures responded more strongly to variation in temperature than northern areas with lower average temperatures.

In line with the findings here for age-0 sandeel, previous studies that have used either recruitment numbers from stock assessment models or indices of recruitment (i.e. larvae abundance) have failed to establish robust direct relationships with

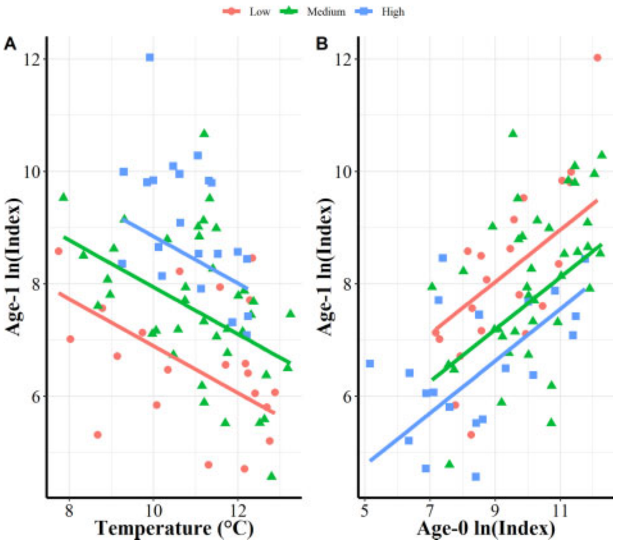

Figure 3. Observed (points) and model predicted (lines) of sandeel abundance (age-1). (A) Relationship between ln(age-1 index) and temperature during the early part of the overwintering period (T_8). Predictions are shown for low (red; below 1st quartile), medium (green; between 1st and 3rd quartiles), and high (blue; above 3rd quartile) recruitment, respectively. (B) Relationship between ln(age-1 index) and ln(age-0 index) in the preceding year (i.e. proxy for previous year's recruitment). Predictions are shown for low (red), medium (green), and high (blue) temperature (T_8).

temperature (Lynam *et al.*, 2013; Carroll *et al.*, 2017; Eerkes-Medrano *et al.*, 2017). In contrast, studies using recruitment per spawner biomass, based on output from stock assessment models, have found negative relationships with temperature (Arnott and Ruxton, 2002; Lindegren *et al.*, 2018). This inconsistency could potentially be attributed to the inclusion of spawning stock biomass when calculating recruitment per spawner, which emphasizes a relatively distinct underlying stock–recruitment relationship. Assuming such a relationship, as in a Ricker model, has been debated on several occasions in relation to short-lived species (Vert-Pre *et al.*, 2013; Szuwalski *et al.*, 2015). Hence, in the present study, we chose not to force the model by making assumptions regarding the stock–recruitment relationship. The above-mentioned inconsistency, could, however, also be attributed to differences in time-series lengths, the data sources, the spatial resolution of the data, or the model approaches.

A significant positive effect of fish length on abundance of age-0 sandeel was found. Different mortality pathways have been proposed for first-feeding larvae (Wright and Bailey, 1996; Henriksen *et al.*, 2018), the larval drift phase (Gurkan *et al.*, 2012, 2013), and overwintering of post-settled juveniles (van Deurs *et al.*, 2011b; MacDonald *et al.*, 2018). The size of age-0 was measured only in winter, which makes it difficult to favour any particular mechanism, but theory about early life and recruitment in fish provide insights to the processes that might be involved. For example, findings could potentially be supported by the classical "Stage-Duration" hypothesis (Anderson, 1988), implying that "bigger is better" and fast growth improves survival early in life (Miller *et al.*, 1988). Bigger is also better for avoiding the starvation of settled juveniles, since mass-specific metabolism during overwintering decrease with increasing size (van Deurs *et al.*, 2011b). Thus, important factors affecting the survival of sandeel during the first year of life are likely to be associated with changes in food condition and predation mortality (Eliasen *et al.*, 2011; MacDonald *et al.*, 2018, 2019). A potential close relationship with *Calanus* copepods has been investigated on several occasions (van Deurs *et al.*, 2009, 2014, 2015), where in particular "match-mismatch" (Cushing, 1990) relationships between the production of *Calanus* eggs and larval hatching have been highlighted (van Deurs *et al.*, 2009; Régnier *et al.*, 2017). The physical oceanography that dictates the conditions for growth and survival during the larval development (Henriksen *et al.*, 2018), including successful retention near suitable habitats (Gurkan *et al.*, 2013), seem to be a key driver for these interlinked relationships. Although no direct effect of temperature was found, recent evidence suggests that temperature can have an indirect pathway influencing the timing of sandeel hatching. Temperature affects the physiological rates in adult sandeel, with warming delaying ovarian development (Wright *et al.*, 2017a) and bringing about earlier hatching of eggs due to faster development rates (Régnier *et al.*, 2018). In addition, the indirect impact of elevated temperatures on food

Table 3. Summary statistics from mixed effects models fitted to data from each of the nine subareas (*n* designates the length of the survey time series of each subarea).

			Fixed effects				SD estimates	
Subarea	n	R^2_m/R^2_c	Slope (T_8)	*p*-value (T_8)	Slope (ln I_{0y-1})	*p*-value (ln $I_{0,y-1}$)	Random effect of year	Residual error
1	14	0.45/0.63	−0.729 (0.370)	0.049*	0.444 (0.226)	0.049*	0.410	0.584
2	8	0.27/0.51	−0.623 (0.651)	0.339	0.163 (0.396)	0.679	0.466	0.666
3	8	0.54/0.56	−0.336 (0.339)	0.322	0.522 (0.202)	0.009**	0.102	0.461
4	5	0.18/0.33	−0.379 (0.998)	0.704	0.309 (0.335)	0.356	0.333	0.695
5	13	0.64/0.70	−0.456 (0.265)	0.086	0.534 (0.116)	<0.001***	0.208	0.476
6	10	0.51/0.59	−0.801 (0.343)	0.019*	0.522 (0.268)	0.052	0.305	0.699
7	12	0.38/0.59	−0.966 (0.428)	0.024*	0.411 (0.284)	0.147	0.530	0.726
8	7	0.73/0.80	−0.801 (0.308)	0.009**	0.869 (0.308)	0.005**	0.245	0.441
9	4	0.94/0.95	0.332 (0.584)	0.569	0.867 (0.134)	<0.001***	0.131	0.367

Fixed effects were based on the final best age-1 model, which included temperature (T_8) and recruitment of age-0 fish in the preceding year (ln$I_{0,y-1}$). The variance explained for fixed effects (R^2_m), combined fixed and random effects of year (R^2_c), slope coefficients, and *p*-values (Wald *Z*-statistics) are presented. Numbers in parentheses are SE for estimated fixed effect slopes.

*$p < 0.05$,

**$p < 0.01$,

***$p < 0.001$,

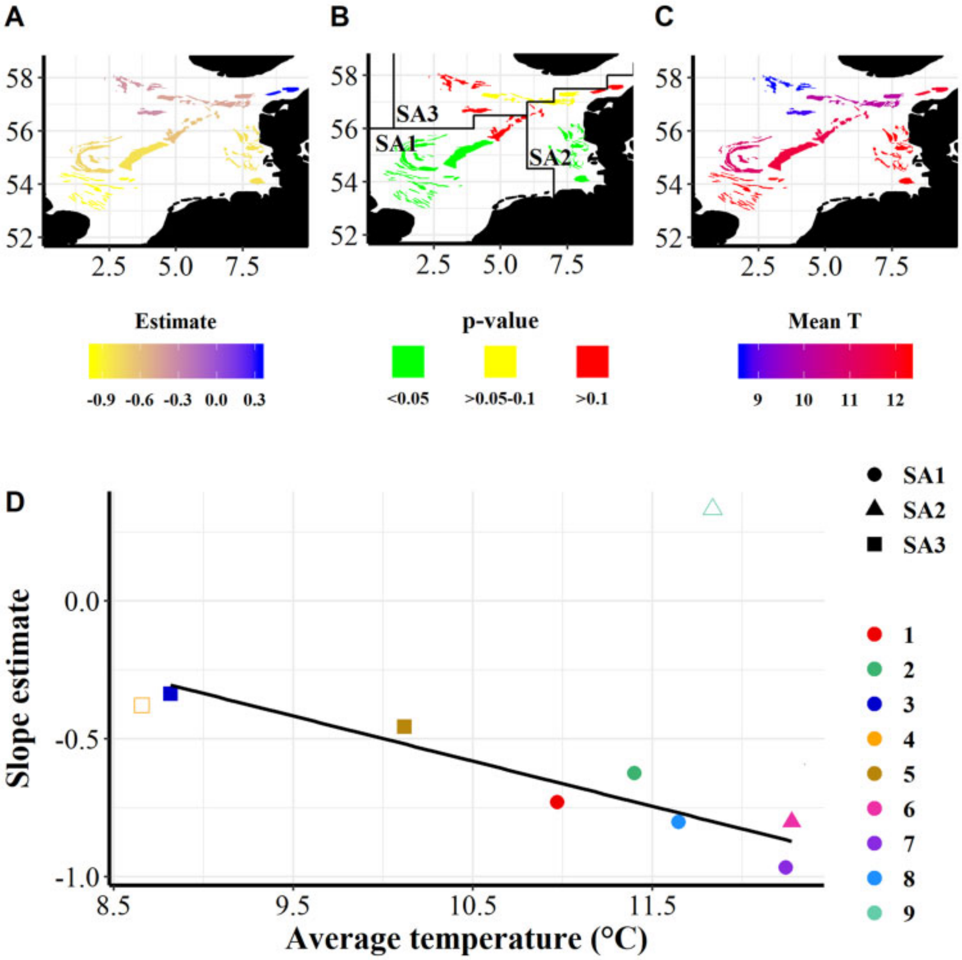

Figure 4. Maps showing spatial variation in average temperature, slopes, and *p*-values (A–C). Relationship between slope coefficients and the average temperature (D). Each point in (D) represents a subarea. Subareas with fewer than 7 years of data are indicated by open dots. The regression line was fitted to subareas with at least 7 years of data (solid dots). The temperature used in (C) and (D) is T_8 averaged across all years. ICES management areas are indicated by the shape of the symbols in (D) and depicted in (B).

availability has been linked to increasing probabilities of trophic mismatch with available prey (Régnier *et al.*, 2019). However, correlation approaches, such as in the present study, are not expected to provide strong evidence for the underlying mechanisms or to map out complicated causation chains. On that note, while results presented here only were designed to detect and identify which sandeel life phases might be sensitive to future impacts of climate change, the analyses do not account for non-linear responses to temperature. However, such responses have been highlighted for several marine fish (Ciannelli *et al.*, 2004, 2012; Katara *et al.*, 2011; Arula *et al.*, 2016), including sandeel (van der Kooij *et al.*, 2008; Lynam *et al.*, 2013; Lindegren *et al.*, 2018; Régnier *et al.*, 2019). The decision to use linear models was based on the length of the time series, which are considerably shorter than in the before-mentioned studies (i.e. degrees of freedom would decrease rapidly if additional parameters to model curvatures or smoother functions were to be included in the models). An alternative non-biological explanation for the strong relationship with length could be the existence of length-dependent catchability in the survey. For example, if catchability increases with size, more fish of a given age group will be caught in years where they grow faster. However, size-dependent catchability of the sandeel dredge was investigated in 2013 and found not to be a problem (Johnsen and Harbitz, 2013). Regarding the potential relationship between temperature and fish length, such a relationship was only found to be significant in one out of nine subareas (Supplementary Figure S7). Nonetheless before making firm conclusions, we recommend that future work should be more comprehensive using model approaches that fits multiple drivers of non-linear relationships (Guisan *et al.*, 2002; Venables and Dichmont, 2004; Boyd and Brown, 2015), but also advanced spatial modelling (Blangiardo *et al.*, 2013) should be considered.

Clear stock–recruitment relationships were not detected. In general, very weak spawner–recruit relationships are a common feature for short-lived species, where recruitment dynamics appear to be driven mainly by environmental variation when the spawning biomass is above some critical lower threshold (Cury *et al.*, 2014; Somarakis *et al.*, 2019). Despite these notions, it seems unrealistic to assume no relationship at all (Hilborn *et al.*, 2017). In models presented here, we therefore used age-1 abundances in the previous year as a proxy for the size of the local spawning stock. This proxy is obviously not capturing the full spawning stock biomass, as it neglects older individuals and weight at age. However, since ICES relies only on the abundance of age-0 and age-1 from the dredge survey, it was decided to do the same in the present study. In addition, the linear models used may have prevented us from detecting the presence of any strong density-dependent relationship (i.e. Ricker-type relationships). An alternative explanation for the absence of a stock–recruitment relationship may involve the relative fine spatial scale of the study. The different subareas may simply have been too small, as indicated by recent studies, revealing that mixing during the larval phase may take place across distances of up to 200 km (Wright et al., 2019) and that only a very weak genetic population structure exists across the North Sea (Jiménez-Mena *et al.*, 2020). Hence, if the exchange of larvae between subareas was substantial enough, detection of local stock–recruitment relationships would be improbable.

Density-dependent recruitment regulation exerted by the abundance of age-1 sandeel was not detected in the present study. This contradicts previous studies using outputs from assessment models (van Deurs *et al.*, 2009; Lindegren *et al.*, 2018). However, a more recent study, based on commercial catch rates (as an indicator of abundance) and a spatial resolution similar to the present study (Rindorf *et al.*, 2019), confirms the lack of significant density-dependent recruitment regulation from the previous cohort. These inconsistencies between studies remain unresolved.

Higher bottom temperature during the beginning of the overwintering period significantly decreased the abundance of age-1 sandeel across the North Sea. This study was not designed to test the underlying mechanisms behind this relationship. Thus, knowledge from the previous work presented here aid in inferring possible causal relationships. Energy budget modelling has suggested that starvation and/or predation, not temperature, are the two main factors driving the survival of older sandeel (MacDonald *et al.*, 2018) and no direct effect of temperature on the survival of age-1 overwintering sandeel has been confirmed (MacDonald *et al.*, 2019). The experimental studies to date have not investigated the lethal effects of temperature accounting for food limitation and predation. Nevertheless, these studies did find that temperature had a negative effect on individual mass change during overwintering (Wright *et al.*, 2017a, b), which supports notions about increased energetic cost of overwintering (van Deurs *et al.*, 2011b). Sandeel is entirely dependent on the storage of energy reserves for both survival and gonad development (Boulcott and Wright, 2008) and warming imposes an extra cost to maintain standard metabolic rate during the overwintering period. As a result, mature individuals reduce investments in gonads rather than compromising the energy for survival at higher temperatures (Wright *et al.*, 2017a, b). Maturation is possible already during the first year but is highly dependent on growth rate, which varies across the North Sea (Bergstad *et al.*, 2001; Boulcott *et al.*, 2007). Southerly areas seem to have populations that mature earlier with nearly 100% already matured at age-1, whereas in northern areas proportion mature are 58–79% (Boulcott *et al.*, 2007). Hence, the increased energetic costs associated with early maturation in southern areas may increase the sensitivity of these populations to elevated temperatures. Moreover, recent evidence on temperature delaying oocyte development in females (Wright *et al.*, 2017a), as well as speeding up development of demersal eggs (Régnier *et al.*, 2018), could have detrimental impacts through the mismatch between key life history events (e.g. spawning and hatching) and food availability (Régnier *et al.*, 2017, 2019). These mechanisms could also be related to the relationship observed for age-0 sandeel here, where lower sandeel abundance is associated with smaller body size. Furthermore, if high water temperatures in autumn and winter force the sandeel to shorten the duration of the overwintering period for reasons related to bioenergetics (van Deurs *et al.*, 2010, 2011b), this may increase predation and fisheries mortality and reduce abundances of sandeel. As a consequence of ocean warming, several marine species interacting with sandeel (via predation or competition) have either increased in abundance or expanded their distributions in the North Sea (Attrill *et al.*, 2007; ter Hofstede *et al.*, 2010; Petitgas *et al.*, 2012; Cormon *et al.*, 2016). The predation pressure on sandeel, especially from other fish species, is already expected to be high (Heath *et al.*, 2009), where the removal by predatory fish alone greatly exceeds that of fisheries, seabirds, and marine mammals combined (Engelhard *et al.*, 2014). Assuming that food intake may increase with temperature if food processing time is not a limiting factor (Reilly *et al.*, 2014), then predation from so-called “aggregative responses” can have great impact on local sandeel biomasses (Temming *et al.*, 2004, 2007), where southern areas might be more vulnerable to such pressures. Fisheries may also act in synergy with these effects, where few exploited populations comprise fish over 4 years old (Bergstad *et al.*, 2002; Rindorf *et al.*, 2016), and as a consequence, most individuals are unlikely to reproduce many times during life. If temperature causes sandeels to mature early, then the impacts on the physiological development of age-1 sandeel, which still need to invest substantial energy in growth during the feeding season (van Deurs *et al.*, 2013), can be driving the trade-offs of allocating energy to gonad development and somatic maintenance (Wright *et al.*, 2017a). Since the majority of exploited spawning stock biomasses in the North Sea is composed mainly of age-1 individuals (ICES, 2016), these processes can potentially cause large proportions of a population to skip spawning, and thus, exploited populations may be more vulnerable to warming.

The effect of temperature was strongest in the southern half of the North Sea. The North Sea can, in terms of temperature, be divided into a northerly cold region and a southerly/coastal warmer region (see Figure 4). The latter are shallow and also largely devoid of thermoclines (Luyten *et al.*, 2003). These features make the area particularly susceptible to ocean warming, and as a result, the North Sea demersal fish assemblages are responding by moving to deeper waters (Dulvy *et al.*, 2008), while sandeel cannot respond accordingly. The distinct life history characteristics of burying behaviour and strong site fidelity increase the vulnerability of sandeel to climate change. Hence, the current warming of the North Sea is expected to impact sandeel populations also in the coming decade, possibly threatening the viability in stable sandeel populations in southern areas. In contrast, the north-eastern sandeel habitats are situated in deeper waters (Rindorf *et al.*, 2016), where thermoclines offer colder bottom temperatures throughout the year, making these areas possibly more resilient to future warming oceans.

Investigating the effect of temperature on different life phases and spatial scales is crucial to determine the likely impact of climate change on the dynamics of marine fish stocks. The insights from the present study made it possible to unravel spatial differences in how temperature influences recruitment and young adults. Furthermore, the local scale of the study enabled us to infer local differences of sandeel in the vulnerability to future warming events in the North Sea ecosystem. The study emphasizes the need for further investigations as the direct link between temperature and overwintering mortality has yet to be verified experimentally and interaction with other drivers such as climate-induced spatial–temporal shifts in the distribution of predatory species remain elusive.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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