



## Productivity and recovery of forage fish under climate change and fishing: North Sea sandeel as a case study

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4 **1 Productivity and recovery of forage fish under climate change and fishing:**

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7 **2 North Sea sandeel as a case study**

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13 **4 MARTIN LINDEGREN<sup>1,2\*</sup>, MIKAEL VAN DEURS<sup>2</sup>, BRIAN R. MACKENZIE<sup>2</sup>, LOTTE**

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37 **13 RUNNING HEAD: Productivity and recovery of forage fish**

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4 20 **ABSTRACT**  
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7 21 Forage fish occupy a central position in marine food-webs worldwide by mediating the transfer of  
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9 22 energy and organic matter from lower to higher trophic levels. The lesser sandeel (*Ammodytes*  
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11 23 *marinus*) is one of the ecologically and economically most important forage fish species in the  
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13 24 North-east Atlantic, acting as a key prey for larger fish and sea birds, as well as supporting a large  
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15 25 commercial fishery. In this case study, we investigate the underlying factors affecting recruitment  
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17 26 and how these in turn affect productivity of the North Sea sandeel using long-term data and  
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19 27 modelling. Our results demonstrated how sandeel productivity in the central North Sea (Dogger  
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21 28 Bank) depends on a combination of external and internal regulatory factors, including fishing and  
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23 29 climate effects, as well as density dependence and food availability of the preferred zooplankton  
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25 30 prey (*Calanus finmarchicus* and *Temora longicornis*). Furthermore, our model scenarios suggest  
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27 31 that while fishing largely contributed to the abrupt stock decline during the late 1990s and the  
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29 32 following period of low biomass, a complete recovery of the stock to the highly productive levels of  
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31 33 the early 1980s would only be possible through changes in the surrounding ecosystem, involving  
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33 34 lower temperatures and improved feeding conditions. To that end, we stress the need for ecosystem-  
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35 35 based management accounting for multiple internal and external factors occurring within the  
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37 36 broader context of the ecosystem in which forage fish species, such as sandeel, play an important  
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39 37 and integral part.  
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52 40 **KEY WORDS:** population dynamics, recruitment, modelling, climate change, fisheries  
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54 41 management  
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## 43 1. INTRODUCTION

44 Forage fish occupy a central position in marine food-webs worldwide (Cury *et al.*, 2000; Checkley *et al.*, 2009). By feeding on zooplankton and acting as a primary prey for large fish, marine birds and mammals, these fish species effectively mediate the transfer and flow of energy and organic matter from lower to higher trophic levels in marine ecosystems. Furthermore, these small, fast growing and typically short-lived species usually show highly variable population dynamics, both in terms of individual growth and recruitment (Checkley *et al.*, 2009; MacKenzie *et al.*, 2012; Lindegren and Checkley 2013; Bartolino *et al.*, 2014). Since only a few species dominate these mid-trophic levels, important ecosystem functions and services (including both supporting and provisioning services such as food for naturally occurring predators and for human consumption) are highly sensitive to changes in the abundances of these species (Cury *et al.*, 2000; Engelhard *et al.*, 2014; Lindegren *et al.*, 2016). Therefore, understanding the underlying factors regulating their large-scale fluctuations and population dynamics is utterly important.

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57 Several studies have demonstrated clear top-down fishing effects on forage fish, usually exemplified by the dramatic collapses of commercially important small pelagic fish stocks of herring, sardines and anchovies (e.g., Dragesund *et al.*, 1980; Coetzee *et al.*, 2008; Freon *et al.*, 2008). In addition, bottom-up forcing, mediated through direct physiological responses to environmental factors or indirect responses to climate-driven changes in the composition and availability of zooplankton prey has been shown to underlie large-scale fluctuations of forage fish, such as the alternating dominance of sardines and anchovies in upwelling systems (Baumgartner *et al.*, 1992; Schwartzlose *et al.*, 1999; Alheit and Niquen 2004; van der Lingen *et al.*, 2006; Checkley *et al.*, 2017). Although many studies have identified single drivers, the potential synergy of multiple

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4 66 internal and external factors in regulating population dynamics of forage fish, as well as their  
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6 67 relative importance throughout ontogeny is a largely unresolved issue (Hjermann *et al.*, 2004;  
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8 68 Lindegren *et al.*, 2011; 2013). Given the ecological importance and high socio-economic value of  
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10 69 forage fish worldwide, an ecosystem-based management approach, taking into consideration  
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12 70 multiple external and internal regulating processes, is necessary to promote sustainable exploitation  
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14 71 of these important marine resources and the diverse set of higher trophic level predators they  
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16 72 support (McLeod and Leslie 2009).  
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23 74 The lesser sandeel (*Ammodytes marinus*) is one of the ecologically and economically most  
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25 75 important forage fish species in the North-east Atlantic, acting as the preferred prey for predatory  
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27 76 fish, marine mammals and birds, as well as supporting a large and lucrative fishery (Furness 2002;  
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29 77 Greenstreet *et al.*, 2006; Engelhard *et al.*, 2014; Dickey-Collas *et al.*, 2014). The industrial sandeel  
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31 78 fishery began in the 1960s, when it mainly targeted sandeel populations in the North Sea. At its  
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33 79 peak in the 1990s this largely unregulated fishery was removing a sandeel biomass amounting to ~1  
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35 80 million tonnes per year. In the early 2000s, the stock biomass declined rapidly and so did the  
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37 81 landings and profitability of the fishery (Dickey-Collas *et al.*, 2013; Engelhard *et al.*, 2014; Fig. 1a,  
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39 82 b). In order to promote stock recovery, the fishery has been under quota regulations for almost a  
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41 83 decade, yet stock biomass has remained low and not returned to the productive levels of the 1980s  
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43 84 (van Deurs *et al.*, 2009; Lynam *et al.*, 2013; Engelhard *et al.*, 2014; ICES 2017). Lesser sandeel in  
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45 85 the central North Sea spend most of the year buried within the bottom sediment (Wright *et al.*,  
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47 86 2000; van Deurs *et al.*, 2011). The growth period is confined to spring when they resurface and feed  
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49 87 on copepods, such as the large *Calanus* sp. and the medium sized *Temora longicornis* (Macer 1966;  
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51 88 van Deurs *et al.*, 2013, 2014). Although a large number of factors have been proposed as drivers of  
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53 89 the population dynamics of sandeel, including biotic processes (Arnott and Ruxton 2002a;  
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4 90 Frederiksen *et al.*, 2007; Dickey-Collas *et al.*, 2013; van Deurs *et al.*, 2013; Eigaard *et al.*, 2014), as  
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6 91 well as climate forcing and fishery effects (Berntsen *et al.*, 1994; Arnott and Ruxton 2002b;  
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8 92 Frederiksen *et al.*, 2007; van Deurs *et al.*, 2009; Eliassen *et al.*, 2011, van Deurs *et al.*, 2014) the  
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10 93 ultimate mechanisms preventing stock recovery are largely unknown, let alone quantified. In this  
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12 94 study, we investigate the underlying factors regulating recruitment and productivity of sandeel in  
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14 95 the central North Sea (Dogger bank) and assess the productivity and recovery potential of the stock  
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16 96 under different climate and fishing scenarios using a coupled modelling approach. Understanding  
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18 97 the combination and potential synergy of these internal and external factors is a prerequisite for  
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20 98 development of ecosystem-based management practices necessary to promote sustainable  
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22 99 exploitation of sandeel and other marine living resources worldwide (McLeod and Leslie 2009).  
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## 30 101 **2. MATERIAL AND METHODS**

### 31 32 33 102 **2.1. Data availability**

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36 103 A number of variables characterising the local physical conditions, as well as regional ocean-  
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38 104 atmospheric forcing, were collected (Table 1). The local climate conditions were represented by  
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40 105 average sea surface temperatures (SST) at the Dogger Bank in each year and quarter, based on the  
41  
42 106 Hadley centre observational data set available on a one-degree grid cell resolution (Fig. 1c), as well  
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44 107 as mean annual sea bottom temperatures available from ICES (<http://ecosystemdata.ices.dk/>). In  
45  
46 108 order to represent regional ocean-atmospheric forcing acting at larger spatial scales, we included  
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48 109 annual averages of the North Atlantic Oscillation Index (NAO), representing the leading Empirical  
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50 110 Orthogonal Function (EOF) of sea level pressure over the Atlantic sector (20°-80°N, 90°W-40°E).  
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53 111 The number of recruits at age zero (“0-group”; R) and spawning stock biomass (SSB) estimates  
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56 112 were derived from stock assessments for the years 1983-2015 of sandeel in the Dogger Bank (Fig.  
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4 113 1a, b), i.e., representing sandeel assessment area 1 (ICES 2017; see also Fig. S1). To account for  
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6 114 density-dependent effects on sandeel recruitment (Arnott & Ruxton 2002a), the number of one-year  
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8 115 old individuals was included. Finally, the abundances of the key zooplankton prey species *Calanus*  
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10 116 *finmarchicus* and *Temora longicornis* (Fig. 1d) in the Dogger Bank area in each quarter were  
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12 117 available from the long-term monitoring of the Continuous Plankton Recorder (CPR; Batten *et al.*,  
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14 118 2003; Johns 2017).  
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## 21 120 **2.2. Statistical analysis and recruitment modelling**

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24 121 Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990; Wood 2006) were used to  
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26 122 examine the relationship between sandeel recruitment success (R/SSB) and the set of biotic and  
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28 123 abiotic variables chosen as possible predictors during model fitting and selection. The following  
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30 124 linearized Ricker formulations with log-transformed recruitment success estimates as responses  
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32 125 were used:  
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$$36 126 \log(R/SSB)_t = a + s(\log(SSB_t)) + s(\log(N1_t)) + s(V_t) + \varepsilon \quad (1)$$

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39 127 where  $a$  is the intercept,  $s$  the thin plate smoothing function, SSB the spawning stock biomass, N1  
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41 128 the number of one-year olds,  $V$  a number of selected climate predictors potentially affecting sandeel  
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43 129 recruitment success (Table 1 ) and  $\varepsilon$  the error term. Although the number of regression splines is  
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45 130 optimized (and penalized) by the generalized cross validation criterion (GCV), the degrees of  
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47 131 freedom of the spline smoother function ( $s$ ) was further constrained to three knots ( $k=3$ ) to allow for  
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49 132 potential nonlinearities, but restrict flexibility during model fitting. Finally, we applied a model  
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51 133 reduction routine based on the GCV and partial  $F$ -tests to find the best possible set of predictors. To  
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53 134 limit the number of candidate models and avoid false positive results arising from multiple model  
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4 135 testing we restricted the set of models to include covariates averaged for the same quarter or as  
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6 136 annual means (Table S2). In addition, we performed a cross validation analysis by fitting the final  
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8 137 model to a randomly selected subset of the data (Picard and Cook 1984), i.e., amounting to 75% of  
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10 138 the observations, and then assessing the predictive accuracy of the models by comparing the  
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12 139 observed values with the predicted recruitment estimates for the remaining subset. The cross-  
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14 140 validation analysis was repeated 1000 times (i.e., with a new set of random and serially independent  
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16 141 draws each time) in order to assess the range of uncertainty associated with the predictions.  
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### 23 143 **2.3. Age-structured model**

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26 144 In order to simulate stock dynamics under different climate and fishing scenarios we applied a  
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28 145 standard age-structured cohort model based on available information and parameters derived from  
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30 146 recent stock assessments (ICES 2017). The simulated population dynamics are represented by  
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32 147 numbers-at-age (N) distributed among 5 age classes (from 0 to 4+), where the so-called plus group  
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34 148 includes all fish 4 years and older. The following formulation was used:  
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$$38 \quad 149 \quad N_{a+1,t+1} = N_{a+1} e^{-(F_{a+1} + M_{a+1})} \quad (2)$$

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42 150 where  $N_{a,t}$  are number-at-age  $a$  in year  $t$ ,  $F_{a,t}$  and  $M_{a,t}$  the fishing mortality and the natural mortality  
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44 151 at age  $a$  in year  $t$ , respectively. The simulations were performed by estimating R/SSB based on the  
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46 152 final S-R model (Eg. 1; Table 3) and the observed values of each covariate in a given year, where  
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48 153 SSB was estimated as the sum of the adult population given by the proportion of mature fish in each  
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50 154 age and year and their corresponding numbers and mean weight-at-age (ICES 2017). In addition, a  
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52 155 stochastic element was included by adding Gaussian noise ( $\epsilon$ ; resampled randomly from the  
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54 156 residuals of the S-R models) to account for unexplained sources of recruitment variability. After  
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4 157 having accounted for intrinsic processes (i.e., growth, maturation, and natural mortality), as well as  
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6 158 external factors (i.e., fishing mortality) in the age-structured cohort models, the forward simulation  
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8 159 loop is reiterated by estimating R/SSB in the following year. Similar to the available stock  
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10 160 assessment model the simulation model applies half-year time steps, where recruitment occurs from  
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12 161 the 1<sup>st</sup> to the 2<sup>nd</sup> part of the year.  
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#### 163 **2.4. Model simulations and scenario testing**

164 To evaluate the relative importance of the various factors affecting sandeel recruitment and survival  
165 we used the model to hindcast the population dynamics over a period from 1996 to 2009 during  
166 which the SSB showed an abrupt decline and subsequently remained at low levels. The hindcast  
167 simulations comprise a control scenario where all input variables (i.e., SST, *C. finmarchicus*, *T.*  
168 *longicornis* and fishing mortalities at age) were kept at observed levels, as well as a set of  
169 “treatments” represented by the following scenarios: (i) reduced F to current levels from 2010 to  
170 2015 (Fig. 1b), (ii) reduced SST to mean levels during the 1980s (Fig. 1c); (iii) introduced high  
171 abundances in *C. finmarchicus* occurring in 1998, 2001, 2004 and 2007 (corresponding to the  
172 observed peak in 1990; Fig. 1d); (iv) and all treatments above (i-iii) together. Furthermore, we  
173 performed multiple stochastic simulations (i.e., by randomly resampling and reintroducing residuals  
174 from the final GAM model) and estimated the probability of collapse as the percentage of  
175 simulations in which SSB falls below the agreed stock reference point below which recruitment is  
176 impaired ( $B_{lim}=160\ 000$  tonnes) for each combination of SST (i.e., ranging from 0 to +2 °C relative  
177 to mean SST) and fishing, given by a scaling factor on mean fishing mortalities-at-age (F) ranging  
178 from 0 to 2 (i.e., representing a fishing closure and doubling of mean Fs, respectively). Probabilities  
179 were based on consecutive SSB values residing below  $B_{lim}$  for a period longer than one generation

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4 180 (i.e., amounting to 4 years). The simulations were initialized at the estimated numbers at age in  
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6 181 2015 run for 30 years, and replicated 1000 times for each combination of  $\Delta$ SST and F multipliers.  
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8 182 While observed SST values were used for model fitting and validation, surrogate time series of SST  
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10 183 were used as input during simulations. Since marine climate is generally positively autocorrelated  
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12 184 (Steele and Henderson 1984), we generated “red-shifted” noise accurately resembling the natural  
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14 185 variability of the observed SST time series by allowing the simulated SST time series to fluctuate  
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16 186 with the same mean, variance and degree of first-year autocorrelation as the observations  
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18 187 (Lindegren *et al.*, 2010). The abundances of *C. finmarchicus* and *T. longicornis* were introduced in  
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20 188 the S-R model by stochastic resampling of observed values in each year due to the lack of a clear  
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22 189 auto-correlated signal. All statistical analyses were conducted using the R software, version 2.15.1  
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24 190 ([www.r-project.org](http://www.r-project.org)).  
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## 192 3. RESULTS

### 193 3.1. Drivers of recruitment success

194 After model fitting and selection the set of covariates retained within the final GAM included  
195 spawning stock biomass (SSB), the number of one-year old sandeel (N1), spring sea surface  
196 temperature (2<sup>nd</sup> quarter) and spring abundances of both *C. finmarchicus* and *T. longicornis* (Table  
197 2; Table S2). Although fitting on variables averaged during winter (1<sup>st</sup> quarter) yielded a slightly  
198 lower GCV (Table S2), the resulting model included a spurious and ecologically unrealistic  
199 negative effect of prey availability (*T. longicornis*) on recruitment success (Fig. S2). The chosen  
200 model, including covariates averaged over spring instead, demonstrated low GCV and a high degree  
201 of explained deviance overall (75.2%). The final relationships between recruitment success,  
202 spawning stock biomass (SSB) and the number of one-year old sandeel (N1) were represented by

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4 203 non-linear or linearly decreasing functions, respectively (Fig. 2a, b), where in the former case the  
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6 204 negative effect on recruitment success is exacerbated at higher values of  $\log(\text{SSB})$ . The functional  
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8 205 relationship between recruitment success and SST was best described by a negative linear  
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10 206 relationship (Fig. 2c), while the effect of *C. finmarchicus* and *T. longicornis* were linear and  
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12 207 positive (Fig. 2d, e). The final model explains the long-term dynamics and inter-annual variability  
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14 208 in recruitment success and hindcasted SSB (based on the age-structured model) well throughout the  
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16 209 period (Fig. 3a, b). Furthermore, the cross-validation routine demonstrated a high degree of  
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18 210 explained deviance for models fitted to a random and serially independent subset of the data, as  
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20 211 well as accuracy in predicting the remaining data (Fig. 4a). In addition, the explained deviance and  
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22 212 significance (p-values) of the model terms remained high when successively fitted and annually  
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24 213 updated with data from 1997 to 2015 (Fig. 4b). Model residuals were normally distributed and  
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26 214 temporally uncorrelated for recruitment and recruitment success (Fig. S3). As a complement to the  
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28 215 GAM approach we provide a number of alternative model formulations based on standard Ricker  
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30 216 models and generalized linear models including polynomial terms to account for non-linear  
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32 217 interactions (Table S2). While the GAM formulation demonstrates the highest degree of explained  
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34 218 deviance, the alternative model formulations demonstrate that the explanatory variables identified in  
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36 219 the GAM approach contribute significantly to the prediction of recruitment and recruitment success  
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38 220 independent of model choice. This supports the robustness of our findings and additionally provides  
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40 221 parameterized models for future management applications.  
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### 50 223 ***3.2. Testing the relative importance of drivers through scenario simulations***

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53 224 The hindcast model simulations used to evaluate the relative importance of the various factors  
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55 225 affecting sandeel recruitment and survival showed that the scenario based on reduced fishing  
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4 226 mortalities lead to a pronounced improvement in stock status relative to the control simulation with  
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6 227 SSB values rising above  $B_{lim}$  throughout most of the period (Fig. 5a). The scenario of reduced SST  
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8 228 demonstrates a more moderate improvement in SSB compared to the control but show SSB values  
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10 229 above  $B_{lim}$  in the early and late 2000s. The scenario introducing recurring high abundances in *C.*  
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12 230 *finmarchicus* shows a rather minor response. Interestingly, the combined scenario introducing all  
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14 231 “treatments” shows considerably higher SSB values well above  $B_{lim}$ . Finally, the model simulations  
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16 232 of sandeel dynamics under different combinations of SST and exploitation illustrate a strong  
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18 233 dependence on both factors with a high probability of collapse at high levels of *F* and SST (Fig. 5b).  
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#### 25 235 **4. DISCUSSION**

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28 236 In this study we have demonstrated how sandeel productivity and the potential for stock recovery in  
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30 237 the Dogger Bank area of the North Sea depend on a combination of internal density-dependent  
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32 238 processes and external environmentally-driven factors. Among the external factors considered in  
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34 239 this study, SST in spring explained a large part of recruitment variability and demonstrated a clear  
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36 240 negative relationship. Consequently, the pronounced long-term increase and unprecedented high  
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38 241 SST values since the early 2000s can partly explain the poor recruitment success and lack of  
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40 242 recovery during recent decades. Furthermore, we show a strong negative relationship between the  
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42 243 abundance of one-year old sandeel and recruitment success (settling of young of the year fish)  
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44 244 indicating pronounced density-dependent regulation, likely acting through food or habitat  
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46 245 competition. The dependence on food availability is supported by the positive effect of *C.*  
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48 246 *finmarchicus* and *T. longicornis* on recruitment success, illustrated by the close correspondence  
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50 247 between peaks in prey abundance with years of high recruitment success. The set of drivers  
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52 248 identified in our study largely corresponds with previous work on sandeel recruitment (Arnott and  
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4 249 Ruxton 2002; van Deurs *et al.*, 2009). This indicates that environmental correlates in relation to  
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6 250 this particular stock appear to be exceptionally robust over time, even when performed on  
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8 251 significantly extended time series and despite a common tendency for published recruitment-  
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10 252 environment correlations to fail when verified upon retest (Myers 1998). Based on this  
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12 253 consistency and the strong support for the drivers and relationships identified we used a scenario-  
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14 254 based modelling approach for assessing how different climate regimes and fishing pressures interact  
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16 255 to determine stock productivity and the potential for stock recovery (Lehodey *et al.*, 2006).  
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18 256 However, before discussing these scenarios, we address the causality between the set of drivers and  
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20 257 their associated effects on recruitment and stock productivity.  
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28 259 First of all, increasing water temperature affects fish metabolism, resulting in higher growth rates, if  
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30 260 food is not a limiting factor and/or if the temperature is not already near the thermal tolerance limit  
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32 261 of the species (Pörtner 2002). In contrast, if food is limiting, growth will decline and the fish may  
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34 262 starve because of increased energetic costs of metabolism. This effect will depend on temperature  
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36 263 as a specific amount of food may be sufficient at low temperatures but cause decreased growth at  
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38 264 high temperatures. Lesser sandeel inhabiting the Dogger area in the North Sea, are not living on the  
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40 265 southern or the northern limit of the distribution range of this species (Jensen *et al.*, 2010; Fishbase  
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42 266 2016). Consequently, the temperatures they experience do not appear to be at, or close to, its  
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44 267 thermal limits. However, the combination of increasing metabolic demands, driven by increasing  
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46 268 temperatures, together with stable or decreasing prey availability (i.e., abundance of *C.*  
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48 269 *finmarchicus* and *T. longicornis*) suggest that food limitation can limit recruitment success and  
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50 270 stock recovery. This is particularly important during late winter and spring as this period covers the  
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52 271 larval phase (Wright and Bailey 1996). Increasing temperatures lead to increasing energy demands  
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54 272 potentially affecting developmental rate of the larvae (Pankhurst and Munday 2011). Furthermore,  
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4 273 in late winter and early spring food is exceptionally scarce and eggs and nauplii of *C. finmarchicus*,  
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6 274 advected into the North Sea from the Atlantic continental shelf, may represent a vital resource for  
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8 275 the newly hatched larvae in this area of the North Sea (Arnott and Ruxton 2002; Richardson *et al.*,  
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10 276 2011). In addition, *T. longicornis* and other medium sized calanoid copepods often serve as other  
11  
12 277 important prey in this area (Macer 1966; van Deurs *et al.* 2014). These copepod species become  
13  
14 278 abundant in late spring, around the time of sandeel metamorphosis, which is another critical life  
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16 279 stage of sandeel (Wright and Bailey 1996). Hence, delayed or suppressed copepod production  
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18 280 during this period may cause starvation and consequently limit survival and year class strength.  
19  
20 281 Although *T. longicornis* is far more abundant than *C. finmarchicus* in late spring (Pitois and Fox  
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22 282 2006), this less abundant prey species may still be important, owing to its larger size and higher fat  
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24 283 content (van Deurs *et al.* 2014).  
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32 285 While these mechanisms stress a strong link between stock productivity and the environment, the  
33  
34 286 long-term increase in SST and decline of *C. finmarchicus* and *T. longicornis* in the North Sea  
35  
36 287 should be understood within the broader context of large-scale ecosystem changes acting across the  
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38 288 North East Atlantic (Beaugrand *et al.*, 2004; Möllmann *et al.*, 2009; Lindegren *et al.*, 2012). These  
39  
40 289 abrupt changes, often referred to as regime shifts, involve a number of additional factors potentially  
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42 290 affecting the population dynamics of sandeel in the North Sea, such as an increasing number of  
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44 291 competing forage fish species and predators on sandeel larvae and juveniles (Raab *et al.*, 2012;  
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46 292 Petitgas *et al.*, 2012; Engelhard *et al.*, 2014) and pronounced shifts in the phyto- and zooplankton  
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48 293 community composition (Reid *et al.*, 1998; Beaugrand 2004; Beare *et al.*, 2004; Jansen and  
49  
50 294 Gislason 2011). These effects are exacerbated by the resident nature of sandeel, which due to its  
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52 295 strong association to a well-defined and patchily distributed habitat (Wright *et al.*, 2000; Jensen *et*  
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4 296 *al.*, 2011) cannot change distribution and take advantage of better conditions elsewhere (Helaouët  
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6 297 and Beaugrand 2007).  
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12 299 After demonstrating the importance of both internal, density-dependent mechanisms and external,  
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14 300 climate-driven factors, including temperature and food availability in regulating sandeel recruitment  
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16 301 (Berntsen *et al.*, 1994; Arnott and Ruxton 2002a; Frederiksen *et al.*, 2007; Dickey-Collas *et al.*,  
17  
18 302 2013; van Deurs *et al.*, 2009; 2013; 2014; Eigaard *et al.*, 2014), the question remains to what extent  
19  
20 303 past changes in these drivers explain the poor productivity and virtual lack of recovery in recent  
21  
22 304 decades. Our scenario-based modelling approach serves to provide insight into this issue by  
23  
24 305 assessing the relative importance of these factors, particularly in relation to commercial fishing. Our  
25  
26 306 results show that fishing largely contributed to the abrupt stock decline during the late 1990s and  
27  
28 307 the following period of low biomass, especially given the extreme fishing mortalities experienced  
29  
30 308 during this period (i.e. mean  $F=1.2$  between 1999 to 2004; Fig. 1b). However, although reducing  $F$   
31  
32 309 to the currently lower levels would likely have maintained the stock biomass above ecologically  
33  
34 310 safe levels (Fig. 5a) a complete recovery of the stock to the highly productive levels of the early  
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36 311 1980s would not have been possible, despite the lower level of exploitation. This highlights that  
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38 312 factors besides fishing also contributed to the stock decline and to maintaining the stock in a state of  
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40 313 poor productivity. We argue that these factors can be explained by the pronounced increase in SST,  
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42 314 the concurrent decline in food availability, as well as the recent increase in natural mortality,  
43  
44 315 especially through predation from mackerel. Whether recruitment and recovery of other sandeel  
45  
46 316 stocks in the area are influenced or limited by the same set of drivers and processes is unclear and  
47  
48 317 merit further attention. However, the joint dependence of recruitment and survival on fishing and  
49  
50 318 environmental factors, including both abiotic and biotic processes, has been shown for several  
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52 319 commercially important forage fish species (Freon *et al.*, 2008; Lindegren *et al.*, 2011, 2013;  
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4 320 Checkley et al., 2017), as well as for large predatory fish stocks worldwide, notably cod (Lindegren  
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6 321 et al., 2009; Gårdmark *et al.*, 2013; Pershing *et al.*, 2015). This supports the generality of our  
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8 322 findings and illustrates the need to adopt a more holistic ecosystem-based approach to fisheries  
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10 323 management, accounting for multiple ecological and physical factors to promote sustainable  
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12 324 exploitation of our living marine resources (MacLeod and Leslie 2009; Long *et al.*, 2015). Despite a  
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14 325 growing body of research on the effect of climate and biotic interactions on fish population  
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16 326 dynamics, only a very limited number of fish stocks worldwide are currently accounting for these  
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18 327 issues in tactical management (Skern-Mauritzen *et al.*, 2015). To that end, we stress the need for  
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20 328 ecosystem-based management accounting for multiple internal and external factors occurring within  
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22 329 the broader context of the ecosystem, in which forage fish species, such as sandeel, play an  
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24 330 important and integral part.  
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4 **TABLES**

5  
6 **Table 1.** Information about the abiotic and biotic covariates used during model fitting with regards to spatial and temporal coverage, as  
7 well as the source of datae.  
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Variable	Month	Area	Data source
SSTQ1	Jan-March	Dogger Bank	<a href="http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html">http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html</a>
SSTQ2	April-June	Dogger Bank	<a href="http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html">http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html</a>
SSTQ3	July-Sept	Dogger Bank	<a href="http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html">http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html</a>
SSTQ4	Oct-Dec	Dogger Bank	<a href="http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html">http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html</a>
SST Annual	Jan-Dec	Dogger Bank	<a href="http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html">http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html</a>
SBT Annual	Jan-Dec	North Sea	<a href="http://ecosystemdata.ices.dk/">http://ecosystemdata.ices.dk/</a>
NAO Annual	Jan-Dec	North Atlantic	<a href="https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based">https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based</a>
<i>C.finmarchicus</i>	Jan-Dec	Dogger Bank	Johns (2017)
<i>T.longicornis</i>	Jan-Dec	Dogger Bank	Johns (2017)

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**Table 2.** Summary statistics of parametric coefficients and smooth terms for the final stock-recruitment model for North Sea sandeel.

A. Intercept

Estimate	SE	t-value	p-value
-0.52	0.1	-5.34	<0.001***

B. Smooth terms

Predictor	edf	F-value	p-value	Partial $r^2$ (%)
SSB	1.71	33.1	<0.001***	52.7
N1	1.00	19.8	<0.001***	18.2
SST	1.00	10.0	0.004**	11.3
<i>C. finmarchicus</i>	1.25	4.53	0.031*	6.5
<i>T. longocornis</i>	1.00	5.89	0.023*	5.7

\* edf is the estimated degrees of freedom for the model smooth terms where edf>1 indicates a non-linear relationship. The partial  $r^2$  refer to the percentage of the total deviance explained by each covariate separately.

**FIGURES CAPTIONS**

**Figure 1.** Long-term trends in (a) sandeel recruitment (grey bars), spawning stock biomass (SSB; black line) and (b) mean fishing mortalities ( $F$  at ages 1-2; grey) estimated from stock assessments (ICES 2017). Horizontal dotted lines represent the precautionary and limiting stock sizes ( $B_{pa}$  and  $B_{lim}$ ). Abiotic and biotic conditions affecting recruitment success and juvenile survival are represented by (c) mean sea surface temperatures (SST) and the abundance of *C. finmarchicus* and *T. longicornis* at the Dogger Bank in spring (April-June) (d).

**Figure 2.** The partial effects of final model predictors on sandeel recruitment success with 95% confidence intervals (grey), illustrating negative relationships between log-recruitment success and spawning stock biomass (SSB) (a), the number of one-year old sandeel (b) and spring sea surface temperature (c), as well as positive effects of prey abundance during spring by *C. finmarchicus* (d) and *T. longicornis* (e).

**Figure 3.** (a) Observed (circles) and fitted values (black) of recruitment success with 95% confidence intervals (grey) based on the final GAM. (b) Observed (circles) and hindcasted estimates of spawning stock biomass (SSB; black) with 95% confidence intervals (grey) based on an age-structured population model.

**Figure 4.** (a) Boxplots of explained deviance from a cross-validation analysis of model fit on a randomly selected subset, as well as the associated accuracy of predictions on the remaining data (after 1000 model iterations). (b) Overall explained deviance (grey) and p-values of the effects of

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4 SSB (solid), abundance at age 1 (dashed) and temperature (dotted) on sandeel recruitment success  
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6 when successively fitting and annually updating the final model on data from 1997 to 2015. (The  
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8 horizontal gray dashed line indicate significance at  $p=0.05$ ).  
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14 **Figure 5.** (a) Hindcast simulations of sandeel SSB based on: (i) observed SST, *C. finmarchicus*, *T.*  
15 *longicornis* and F values (black); (ii) reduced F to current levels (2010-2015) (black dashed); (iii)  
16 reduced SST to mean levels during the 1980s (black dotted); (iv) introduced peaks in *C.*  
17 *finmarchicus* in 1998, 2001, 2004 and 2007 (grey solid); (v) and all changes (ii-iv) together (grey  
18 dashed). The solid horizontal red line marks the limiting stock level ( $B_{lim}$ ). (b) Probability of SSB  
19 falling below  $B_{lim}$  given changes in mean SST (by -1 to 2°C) and fishing, given by a scaling factor  
20 on mean fishing mortalities-at-age (F multiplier) ranging from 0 to 2, hence representing a fishing  
21 closure and doubling of mean F, respectively (where 1 represent F equal to the long-term average,  
22  $F_{age1-2} = 0.71$ ).  
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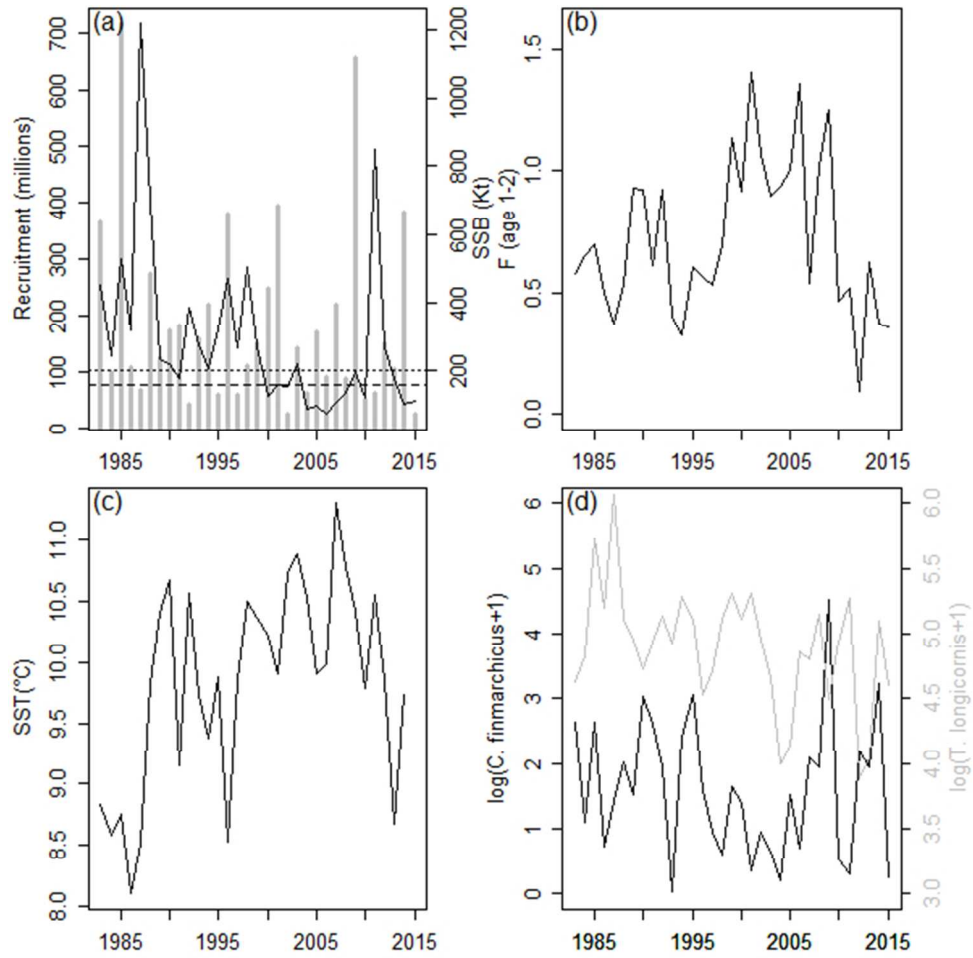


Figure 1

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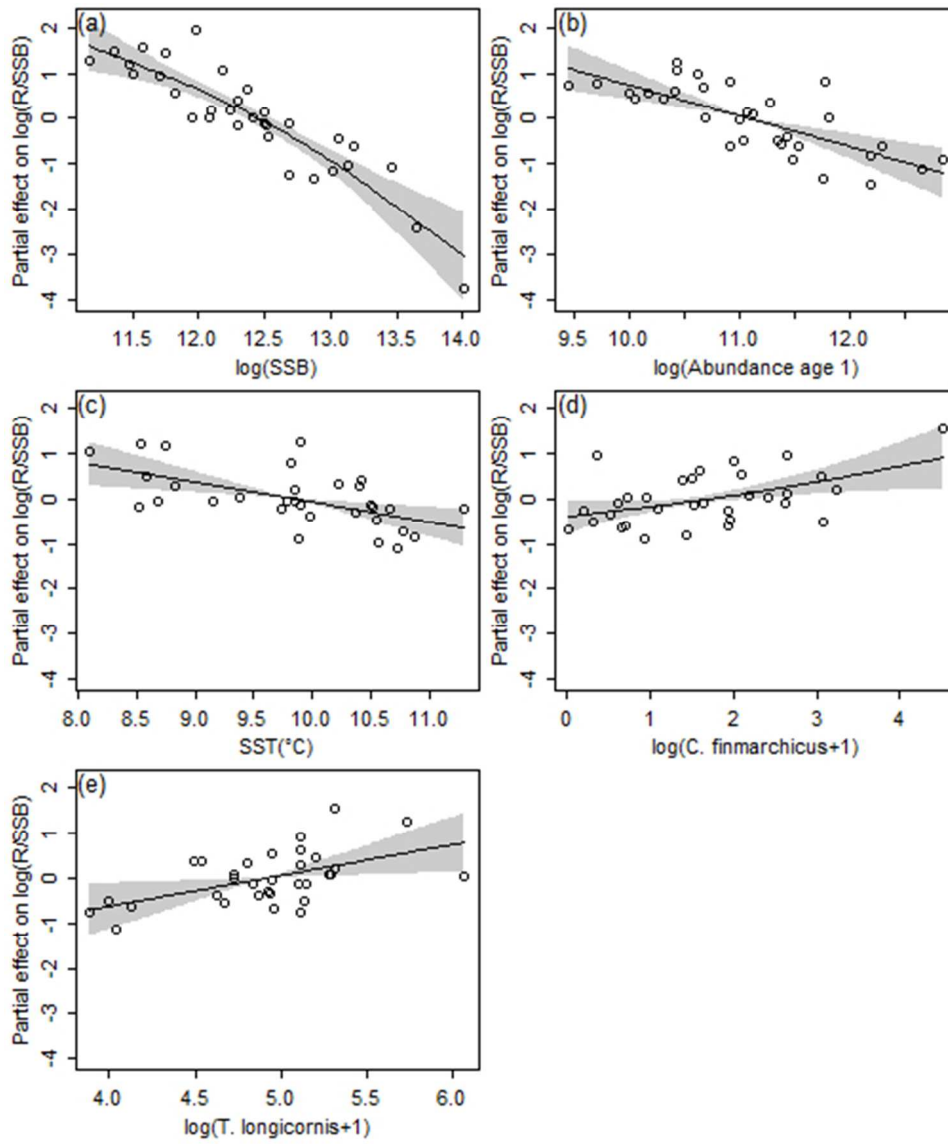


Figure 2

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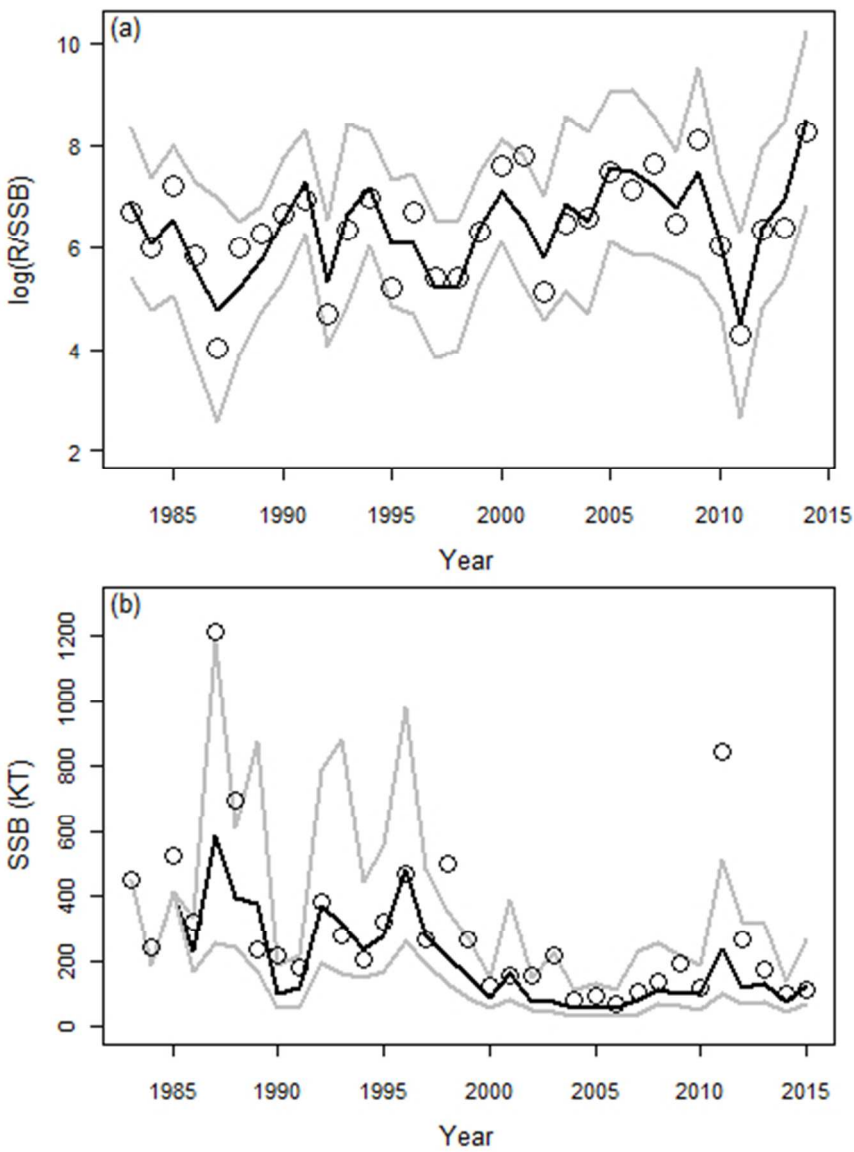


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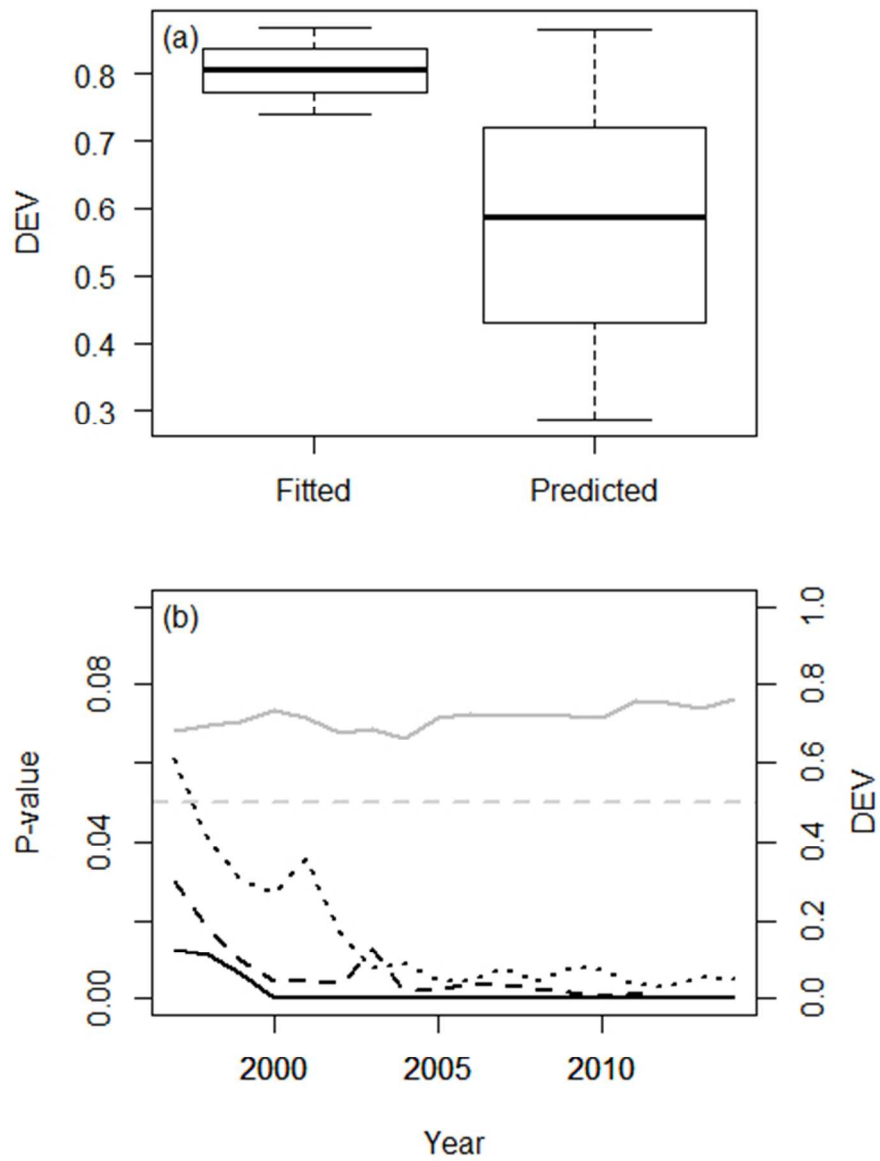


Figure 4

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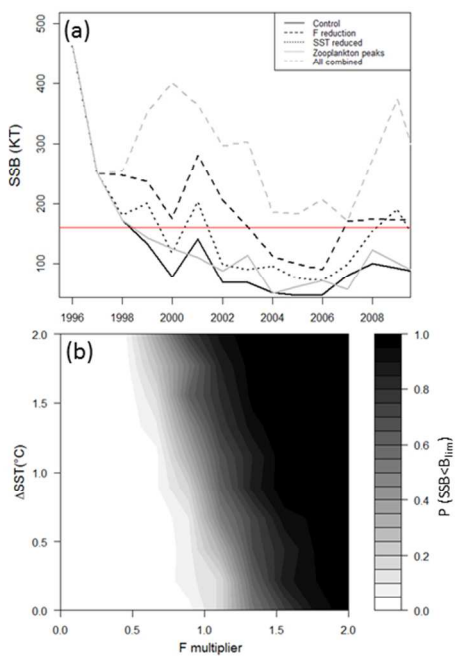


Figure 5

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review

## SUPPLEMENTARY TABLES

**Table S1.** The generalized cross validation scores (GCV) and Akaike's Information Criterion (AIC) after fitting the S-R model to each abiotic covariate and the zooplankton variables (*Calanus finmarchicus* and *Temora longicornis*) in the corresponding quarter (or as annual averages). The selected model is highlighted in bold.

Variable	GCV	AIC
SSTQ1*	0.380	62.6
<b>SSTQ2</b>	<b>0.411</b>	<b>66.7</b>
SSTQ3	0.532	74.8
SSTQ4	0.732	85.8
SSTAnnual	0.443	69.5
SBTAnnual	0.456	70.1
NAOAnnual	0.475	71.5

\*Note that fitting the model on SST and zooplankton in quarter 1 yielded the lowest AIC/GCV. However, the model showed a spurious and ecologically unrealistic negative effect of prey availability (*Temora longicornis*) on recruitment success (Fig. S2) and was therefore excluded.

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**Table S2.** Summary of three alternative model parametric model formulations. Extended Ricker  $\ln(R/S) = c_1S + c_2 \ln(N) + c_3T + c_4Z_1 + c_5Z_2 + k$  (M 1), simple linear regression  $R = c_1S + c_2N + c_3T + c_4Z_1 + c_5Z_2 + k$  (M 2), and second order polynomial  $\ln(R/S) = c_1 \ln(S) + c_2 \ln(S)^2 + c_3 \ln(N) + c_4 \ln(N)^2 + c_5T + c_6Z_1 + c_7Z_2 + k$  (M 3).

The models use the same input as the GAM model in the main text of this manuscript: R (recruitment, in thousands individuals), S (spawning stock biomass, in tons), N (number of age-1 sandeel, in thousands individuals), T (sea surface temperature in °C),  $Z_1$  (CPR index for *Calanus finmarchicus*), and  $Z_2$  (CPR index for *Temora longicornis*). See material and method and Table 1 in the main text for a more detailed description of data sources. The table contains estimated coefficients ( $c_1 - c_7$  and  $k$ ) and the associated p-values (presented within parentheses, alpha = 0.05).

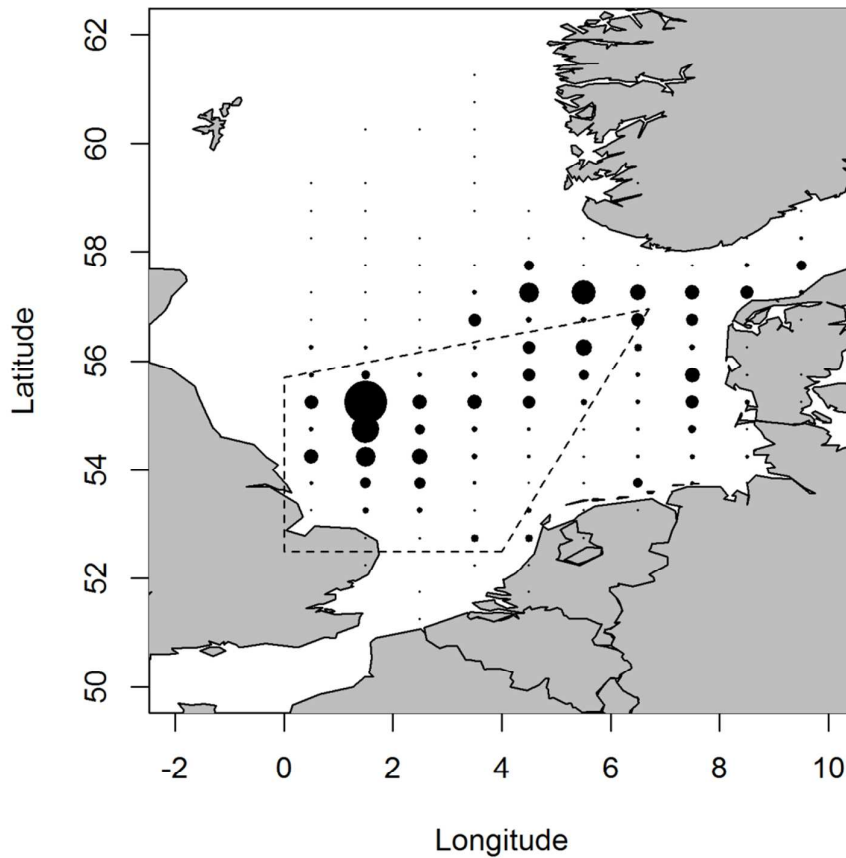
Estimated coefficients:

Model	c1	c2	c3	c4	c5	c6	c7	K	adj.R2
M1	-0.0000046	-0.72	-0.42	-0.22	-0.83			15.43	0.69
M2	-230.5	-843	-74150000	6.356	110800000			421500000	0.36
M3	9.46	-0.44	1.16	-0.085	-0.47	0.22	0.74	-44.45	0.71

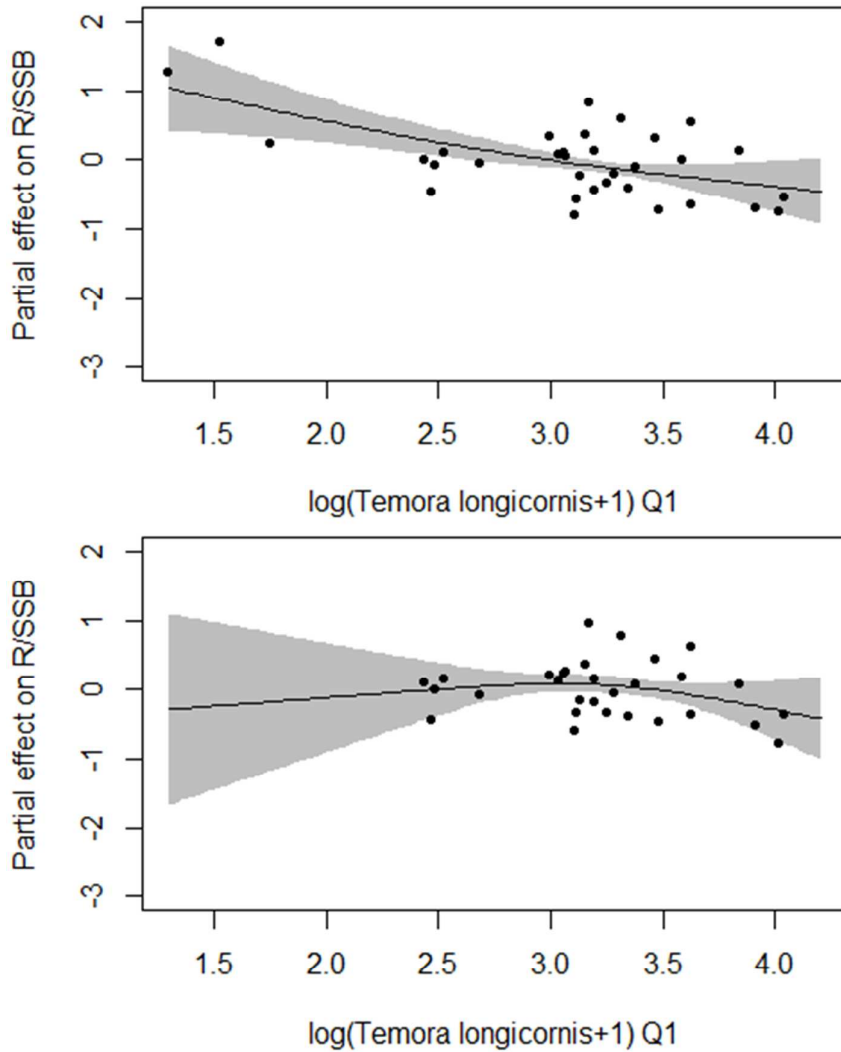
P-values for each coefficient:

Model	c1	c2	c3	c4	c5	c6	c7	K
M1	<0.001***	<0.001***	<0.01**	0.042*	0.01*			<0.001
M2	0.112	0.025*	0.041*	0.017*	0.1			0.334
M3	0.084	0.047*	0.725	0.569	<0.01**	0.072	0.018*	0.298

## SUPPLEMENTARY FIGURES

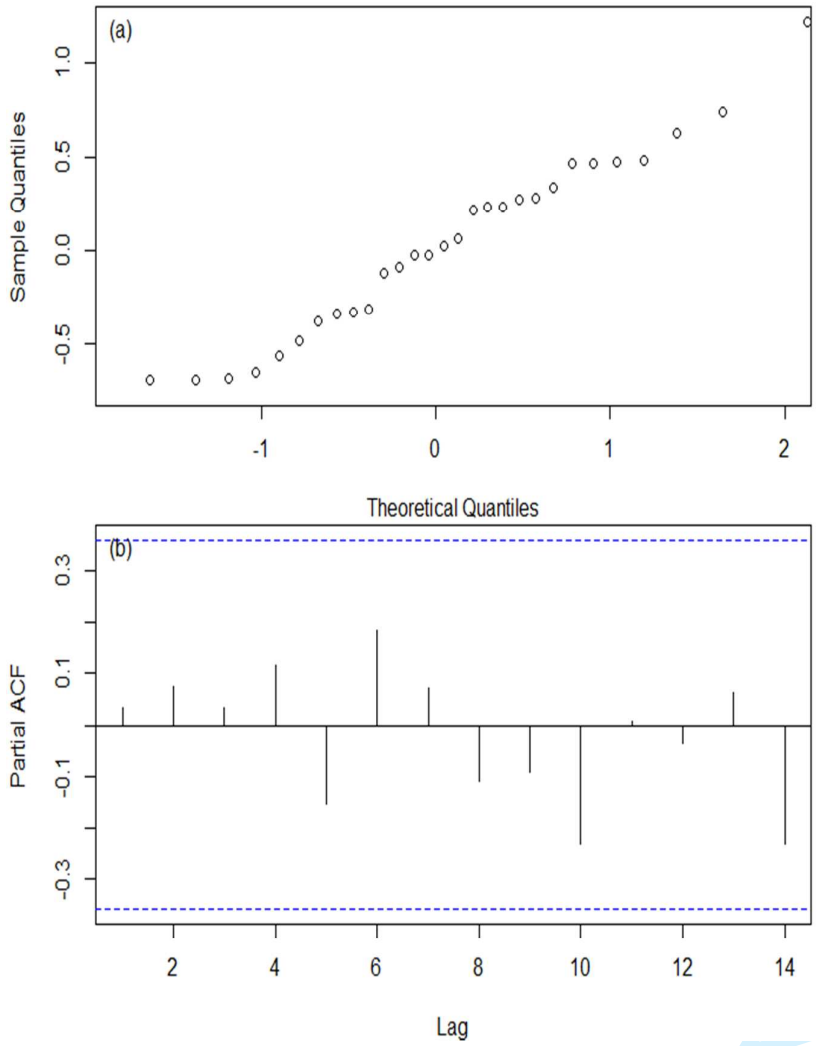


**Figure S1.** Map of the study area. Black round symbols illustrate the relative distributions of sandeel landings since 2003. Box with dashed boundaries envelopes Dogger bank and all landings from sandeel management area 1 (the Dogger bank population).



**Figure S2.** The partial effect of *Temora longicornis* in quarter 1 on sandeel recruitment success.

The model shows a spurious and ecologically unrealistic negative effect of prey availability (upper panel) which is entirely driven by three observations with low zooplankton abundances. If excluding these during fitting the relationship becomes insignificant ( $p=0.49$ ) (lower panel).



**Figure S3.** (A) Normal probability plots and (B) partial autocorrelation plots of the final S-R models for sandeel recruitment success.

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