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Published in:
Fisheries Oceanography

Link to article, DOI:
[10.1111/fog.12246](https://doi.org/10.1111/fog.12246)

Publication date:
2018

Document Version
Peer reviewed version

[Link back to DTU Orbit](#)

Citation (APA):
Lindegren, M., van Deurs, M., MacKenzie, B., Worsøe Clausen, L., Christensen, A., & Rindorf, A. (2018). Productivity and recovery of forage fish under climate change and fishing: North Sea sandeel as a case study. *Fisheries Oceanography*, 27(3), 212-221. <https://doi.org/10.1111/fog.12246>

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

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RUNNING HEAD: Productivity and recovery of forage fish

ABSTRACT

Forage fish occupy a central position in marine food-webs worldwide by mediating the transfer of energy and organic matter from lower to higher trophic levels. The lesser sandeel (*Ammodytes marinus*) is one of the ecologically and economically most important forage fish species in the North-east Atlantic, acting as a key prey for larger fish and sea birds, as well as supporting a large commercial fishery. In this case study, we investigate the underlying factors affecting recruitment and how these in turn affect productivity of the North Sea sandeel using long-term data and modelling. Our results demonstrated how sandeel productivity in the central North Sea (Dogger Bank) depends on a combination of external and internal regulatory factors, including fishing and climate effects, as well as density dependence and food availability of the preferred zooplankton prey (*Calanus finmarchicus* and *Temora longicornis*). Furthermore, our model scenarios suggest that while fishing largely contributed to the abrupt stock decline during the late 1990s and the following period of low biomass, a complete recovery of the stock to the highly productive levels of the early 1980s would only be possible through changes in the surrounding ecosystem, involving lower temperatures and improved feeding conditions. To that end, we stress the need for ecosystem-based management accounting for multiple internal and external factors occurring within the broader context of the ecosystem in which forage fish species, such as sandeel, play an important and integral part.

KEY WORDS: population dynamics, recruitment, modelling, climate change, fisheries management

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1. INTRODUCTION

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.

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

internal and external factors in regulating population dynamics of forage fish, as well as their relative importance throughout ontogeny is a largely unresolved issue (Hjermann *et al.*, 2004; Lindegren *et al.*, 2011; 2013). Given the ecological importance and high socio-economic value of forage fish worldwide, an ecosystem-based management approach, taking into consideration multiple external and internal regulating processes, is necessary to promote sustainable exploitation of these important marine resources and the diverse set of higher trophic level predators they support (McLeod and Leslie 2009).

The lesser sandeel (*Ammodytes marinus*) is one of the ecologically and economically most important forage fish species in the North-east Atlantic, acting as the preferred prey for predatory fish, marine mammals and birds, as well as supporting a large and lucrative fishery (Furness 2002; Greenstreet *et al.*, 2006; Engelhard *et al.*, 2014; Dickey-Collas *et al.*, 2014). The industrial sandeel fishery began in the 1960s, when it mainly targeted sandeel populations in the North Sea. At its peak in the 1990s this largely unregulated fishery was removing a sandeel biomass amounting to ~1 million tonnes per year. In the early 2000s, the stock biomass declined rapidly and so did the landings and profitability of the fishery (Dickey-Collas *et al.*, 2013; Engelhard *et al.*, 2014; Fig. 1a, b). In order to promote stock recovery, the fishery has been under quota regulations for almost a decade, yet stock biomass has remained low and not returned to the productive levels of the 1980s (van Deurs *et al.*, 2009; Lynam *et al.*, 2013; Engelhard *et al.*, 2014; ICES 2017). Lesser sandeel in the central North Sea spend most of the year buried within the bottom sediment (Wright *et al.*, 2000; van Deurs *et al.*, 2011). The growth period is confined to spring when they resurface and feed on copepods, such as the large *Calanus* sp. and the medium sized *Temora longicornis* (Macer 1966; van Deurs *et al.*, 2013, 2014). Although a large number of factors have been proposed as drivers of the population dynamics of sandeel, including biotic processes (Arnott and Ruxton 2002a;

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Frederiksen *et al.*, 2007; Dickey-Collas *et al.*, 2013; van Deurs *et al.*, 2013; Eigaard *et al.*, 2014), as well as climate forcing and fishery effects (Berntsen *et al.*, 1994; Arnott and Ruxton 2002b; Frederiksen *et al.*, 2007; van Deurs *et al.*, 2009; Eliassen *et al.*, 2011, van Deurs *et al.*, 2014) the ultimate mechanisms preventing stock recovery are largely unknown, let alone quantified. In this study, we investigate the underlying factors regulating recruitment and productivity of sandeel in the central North Sea (Dogger bank) and assess the productivity and recovery potential of the stock under different climate and fishing scenarios using a coupled modelling approach. Understanding the combination and potential synergy of these internal and external factors is a prerequisite for development of ecosystem-based management practices necessary to promote sustainable exploitation of sandeel and other marine living resources worldwide (McLeod and Leslie 2009).

2. MATERIAL AND METHODS

2.1. Data availability

A number of variables characterising the local physical conditions, as well as regional ocean-atmospheric forcing, were collected (Table 1). The local climate conditions were represented by average sea surface temperatures (SST) at the Dogger Bank in each year and quarter, based on the Hadley centre observational data set available on a one-degree grid cell resolution (Fig. 1c), as well as mean annual sea bottom temperatures available from ICES (<http://ecosystemdata.ices.dk/>). In order to represent regional ocean-atmospheric forcing acting at larger spatial scales, we included annual averages of the North Atlantic Oscillation Index (NAO), representing the leading Empirical Orthogonal Function (EOF) of sea level pressure over the Atlantic sector (20°-80°N, 90°W-40°E). The number of recruits at age zero (“0-group”; R) and spawning stock biomass (SSB) estimates were derived from stock assessments for the years 1983-2015 of sandeel in the Dogger Bank (Fig.

1a, b), i.e., representing sandeel assessment area 1 (ICES 2017; see also Fig. S1). To account for density-dependent effects on sandeel recruitment (Arnott & Ruxton 2002a), the number of one-year old individuals was included. Finally, the abundances of the key zooplankton prey species *Calanus fincmarchicus* and *Temora longicornis* (Fig. 1d) in the Dogger Bank area in each quarter were available from the long-term monitoring of the Continuous Plankton Recorder (CPR; Batten *et al.*, 2003; Johns 2017).

2.2. Statistical analysis and recruitment modelling

Generalized Additive Models (GAMs; Hastie and Tibshirani, 1990; Wood 2006) were used to examine the relationship between sandeel recruitment success (R/SSB) and the set of biotic and abiotic variables chosen as possible predictors during model fitting and selection. The following linearized Ricker formulations with log-transformed recruitment success estimates as responses were used:

$$\log(R/SSB)_t = a + s(\log(SSB_t)) + s(\log(N1_t)) + s(V_t) + \varepsilon \quad (1)$$

where a is the intercept, s the thin plate smoothing function, SSB the spawning stock biomass, N1 the number of one-year olds, V a number of selected climate predictors potentially affecting sandeel recruitment success (Table 1) and ε the error term. Although the number of regression splines is optimized (and penalized) by the generalized cross validation criterion (GCV), the degrees of freedom of the spline smoother function (s) was further constrained to three knots ($k=3$) to allow for potential nonlinearities, but restrict flexibility during model fitting. Finally, we applied a model reduction routine based on the GCV and partial F -tests to find the best possible set of predictors. To limit the number of candidate models and avoid false positive results arising from multiple model

testing we restricted the set of models to include covariates averaged for the same quarter or as annual means (Table S2). In addition, we performed a cross validation analysis by fitting the final model to a randomly selected subset of the data (Picard and Cook 1984), i.e., amounting to 75% of the observations, and then assessing the predictive accuracy of the models by comparing the observed values with the predicted recruitment estimates for the remaining subset. The cross-validation analysis was repeated 1000 times (i.e., with a new set of random and serially independent draws each time) in order to assess the range of uncertainty associated with the predictions.

2.3. Age-structured model

In order to simulate stock dynamics under different climate and fishing scenarios we applied a standard age-structured cohort model based on available information and parameters derived from recent stock assessments (ICES 2017). The simulated population dynamics are represented by numbers-at-age (N) distributed among 5 age classes (from 0 to 4+), where the so-called plus group includes all fish 4 years and older. The following formulation was used:

$$N_{a+1,t+1} = N_{a,t} e^{-(F_{a,t} + M_{a,t})} \tag{2}$$

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 at age a in year t , respectively. The simulations were performed by estimating R/SSB based on the final S-R model (Eg. 1; Table 3) and the observed values of each covariate in a given year, where SSB was estimated as the sum of the adult population given by the proportion of mature fish in each age and year and their corresponding numbers and mean weight-at-age (ICES 2017). In addition, a stochastic element was included by adding Gaussian noise (ϵ ; resampled randomly from the residuals of the S-R models) to account for unexplained sources of recruitment variability. After

having accounted for intrinsic processes (i.e., growth, maturation, and natural mortality), as well as external factors (i.e., fishing mortality) in the age-structured cohort models, the forward simulation loop is reiterated by estimating R/SSB in the following year. Similar to the available stock assessment model the simulation model applies half-year time steps, where recruitment occurs from the 1st to the 2nd part of the year.

2.4. Model simulations and scenario testing

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

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(i.e., amounting to 4 years). The simulations were initialized at the estimated numbers at age in 2015 run for 30 years, and replicated 1000 times for each combination of Δ SST and F multipliers. While observed SST values were used for model fitting and validation, surrogate time series of SST were used as input during simulations. Since marine climate is generally positively autocorrelated (Steele and Henderson 1984), we generated “red-shifted” noise accurately resembling the natural variability of the observed SST time series by allowing the simulated SST time series to fluctuate with the same mean, variance and degree of first-year autocorrelation as the observations (Lindgren *et al.*, 2010). The abundances of *C. finmarchicus* and *T. longicornis* were introduced in the S-R model by stochastic resampling of observed values in each year due to the lack of a clear auto-correlated signal. All statistical analyses were conducted using the R software, version 2.15.1 (www.r-project.org).

3. RESULTS

3.1. Drivers of recruitment success

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

non-linear or linearly decreasing functions, respectively (Fig. 2a, b), where in the former case the negative effect on recruitment success is exacerbated at higher values of $\log(\text{SSB})$. The functional relationship between recruitment success and SST was best described by a negative linear relationship (Fig. 2c), while the effect of *C. finmarchicus* and *T. longicornis* were linear and positive (Fig. 2d, e). The final model explains the long-term dynamics and inter-annual variability in recruitment success and hindcasted SSB (based on the age-structured model) well throughout the period (Fig. 3a, b). Furthermore, the cross-validation routine demonstrated a high degree of explained deviance for models fitted to a random and serially independent subset of the data, as well as accuracy in predicting the remaining data (Fig. 4a). In addition, the explained deviance and significance (p-values) of the model terms remained high when successively fitted and annually updated with data from 1997 to 2015 (Fig. 4b). Model residuals were normally distributed and temporally uncorrelated for recruitment and recruitment success (Fig. S3). As a complement to the GAM approach we provide a number of alternative model formulations based on standard Ricker models and generalized linear models including polynomial terms to account for non-linear interactions (Table S2). While the GAM formulation demonstrates the highest degree of explained deviance, the alternative model formulations demonstrate that the explanatory variables identified in the GAM approach contribute significantly to the prediction of recruitment and recruitment success independent of model choice. This supports the robustness of our findings and additionally provides parameterized models for future management applications.

3.2. Testing the relative importance of drivers through scenario simulations

The hindcast model simulations used to evaluate the relative importance of the various factors affecting sandeel recruitment and survival showed that the scenario based on reduced fishing

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226 mortalities lead to a pronounced improvement in stock status relative to the control simulation with
227 SSB values rising above B_{lim} throughout most of the period (Fig. 5a). The scenario of reduced SST
228 demonstrates a more moderate improvement in SSB compared to the control but show SSB values
229 above B_{lim} in the early and late 2000s. The scenario introducing recurring high abundances in *C.*
230 *finmarchicus* shows a rather minor response. Interestingly, the combined scenario introducing all
231 “treatments” shows considerably higher SSB values well above B_{lim} . Finally, the model simulations
232 of sandeel dynamics under different combinations of SST and exploitation illustrate a strong
233 dependence on both factors with a high probability of collapse at high levels of *F* and SST (Fig. 5b).
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235 **4. DISCUSSION**

236 In this study we have demonstrated how sandeel productivity and the potential for stock recovery in
237 the Dogger Bank area of the North Sea depend on a combination of internal density-dependent
238 processes and external environmentally-driven factors. Among the external factors considered in
239 this study, SST in spring explained a large part of recruitment variability and demonstrated a clear
240 negative relationship. Consequently, the pronounced long-term increase and unprecedented high
241 SST values since the early 2000s can partly explain the poor recruitment success and lack of
242 recovery during recent decades. Furthermore, we show a strong negative relationship between the
243 abundance of one-year old sandeel and recruitment success (settling of young of the year fish)
244 indicating pronounced density-dependent regulation, likely acting through food or habitat
245 competition. The dependence on food availability is supported by the positive effect of *C.*
246 *finmarchicus* and *T. longicornis* on recruitment success, illustrated by the close correspondence
247 between peaks in prey abundance with years of high recruitment success. The set of drivers
248 identified in our study largely corresponds with previous work on sandeel recruitment (Arnott and

Ruxton 2002; van Deurs *et al.*, 2009). This indicates that environmental correlates in relation to this particular stock appear to be exceptionally robust over time, even when performed on significantly extended time series and despite a common tendency for published recruitment-environment correlations to fail when verified upon retest (Myers 1998). Based on this consistency and the strong support for the drivers and relationships identified we used a scenario-based modelling approach for assessing how different climate regimes and fishing pressures interact to determine stock productivity and the potential for stock recovery (Lehodey *et al.*, 2006). However, before discussing these scenarios, we address the causality between the set of drivers and their associated effects on recruitment and stock productivity.

First of all, increasing water temperature affects fish metabolism, resulting in higher growth rates, if food is not a limiting factor and/or if the temperature is not already near the thermal tolerance limit of the species (Pörtner 2002). In contrast, if food is limiting, growth will decline and the fish may starve because of increased energetic costs of metabolism. This effect will depend on temperature as a specific amount of food may be sufficient at low temperatures but cause decreased growth at high temperatures. Lesser sandeel inhabiting the Dogger area in the North Sea, are not living on the southern or the northern limit of the distribution range of this species (Jensen *et al.*, 2010; Fishbase 2016). Consequently, the temperatures they experience do not appear to be at, or close to, its thermal limits. However, the combination of increasing metabolic demands, driven by increasing temperatures, together with stable or decreasing prey availability (i.e., abundance of *C. finmarchicus* and *T. longicornis*) suggest that food limitation can limit recruitment success and stock recovery. This is particularly important during late winter and spring as this period covers the larval phase (Wright and Bailey 1996). Increasing temperatures lead to increasing energy demands potentially affecting developmental rate of the larvae (Pankhurst and Munday 2011). Furthermore,

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in late winter and early spring food is exceptionally scarce and eggs and nauplii of *C. finmarchicus*,
advected into the North Sea from the Atlantic continental shelf, may represent a vital resource for
the newly hatched larvae in this area of the North Sea (Arnott and Ruxton 2002; Richardson *et al.*,
2011). In addition, *T. longicornis* and other medium sized calanoid copepods often serve as other
important prey in this area (Macer 1966; van Deurs et al. 2014). These copepod species become
abundant in late spring, around the time of sandeel metamorphosis, which is another critical life
stage of sandeel (Wright and Bailey 1996). Hence, delayed or suppressed copepod production
during this period may cause starvation and consequently limit survival and year class strength.
Although *T. longicornis* is far more abundant than *C. finmarchicus* in late spring (Pitois and Fox
2006), this less abundant prey species may still be important, owing to its larger size and higher fat
content (van Deurs *et al.* 2014).

While these mechanisms stress a strong link between stock productivity and the environment, the
long-term increase in SST and decline of *C. finmarchicus* and *T. longicornis* in the North Sea
should be understood within the broader context of large-scale ecosystem changes acting across the
North East Atlantic (Beaugrand *et al.*, 2004; Möllmann *et al.*, 2009; Lindegren *et al.*, 2012). These
abrupt changes, often referred to as regime shifts, involve a number of additional factors potentially
affecting the population dynamics of sandeel in the North Sea, such as an increasing number of
competing forage fish species and predators on sandeel larvae and juveniles (Raab *et al.*, 2012;
Petitgas *et al.*, 2012; Engelhard *et al.*, 2014) and pronounced shifts in the phyto- and zooplankton
community composition (Reid *et al.*, 1998; Beaugrand 2004; Beare *et al.*, 2004; Jansen and
Gislason 2011). These effects are exacerbated by the resident nature of sandeel, which due to its
strong association to a well-defined and patchily distributed habitat (Wright *et al.*, 2000; Jensen *et*

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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.*,
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18 302 2013; van Deurs *et al.*, 2009; 2013; 2014; Eigaard *et al.*, 2014), the question remains to what extent
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20 303 past changes in these drivers explain the poor productivity and virtual lack of recovery in recent
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22 304 decades. Our scenario-based modelling approach serves to provide insight into this issue by
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24 305 assessing the relative importance of these factors, particularly in relation to commercial fishing. Our
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26 306 results show that fishing largely contributed to the abrupt stock decline during the late 1990s and
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28 307 the following period of low biomass, especially given the extreme fishing mortalities experienced
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30 308 during this period (i.e. mean $F=1.2$ between 1999 to 2004; Fig. 1b). However, although reducing F
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32 309 to the currently lower levels would likely have maintained the stock biomass above ecologically
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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,
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44 315 especially through predation from mackerel. Whether recruitment and recovery of other sandeel
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46 316 stocks in the area are influenced or limited by the same set of drivers and processes is unclear and
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48 317 merit further attention. However, the joint dependence of recruitment and survival on fishing and
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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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Checkley et al., 2017), as well as for large predatory fish stocks worldwide, notably cod (Lindegren et al., 2009; Gårdmark *et al.*, 2013; Pershing *et al.*, 2015). This supports the generality of our findings and illustrates the need to adopt a more holistic ecosystem-based approach to fisheries management, accounting for multiple ecological and physical factors to promote sustainable exploitation of our living marine resources (MacLeod and Leslie 2009; Long *et al.*, 2015). Despite a growing body of research on the effect of climate and biotic interactions on fish population dynamics, only a very limited number of fish stocks worldwide are currently accounting for these issues in tactical management (Skern-Mauritzen *et al.*, 2015). To that end, we stress the need for ecosystem-based management accounting for multiple internal and external factors occurring within the broader context of the ecosystem, in which forage fish species, such as sandeel, play an important and integral part.

ACKNOWLEDGEMENTS

The contributions by MvD and BRM in this investigation were supported in part by the COFASP ERA-NET partners, which has received funding from the European Union’s Seventh Framework Programme for research, technological development and demonstration under grant agreement no. 321553 (GOFORIT project), and by the national funding agency of Denmark (Innovationsfonden). MvD was also supported by Management of North Sea sandeel in the years ahead (33113-B-15-002 European Fisheries and Maritime Fund). We also want thank SAHFOS for providing CPR-data and two anonymous reviewers for their insightful and constructive comments.

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4 343 **REFERENCES**
5
6

7 344 Alheit, J. and Niquen, M. (2004) Regime shifts in the Humboldt Current ecosystem. *Progress in*
8
9 345 *Oceanography* 60:201–222.

10
11
12 346 Arnott, S. A., Ruxton, G. D., and Poloczanska, E. S. (2002a) Stochastic dynamic population model
13
14 347 of North Sea sandeels, and its application to precautionary management procedures. *Marine*
15
16 348 *Ecology Progress Series* 235:223-234.

17
18
19
20 349 Arnott, S. A. and Ruxton, G. D. (2002b) Sandeel recruitment in the North Sea: demographic,
21
22 350 climatic and trophic effects. *Marine Ecology Progress Series* 238:199-210.

23
24
25 351 Bartolino, V., Margonski, P., Lindegren, M., Linderholm, H., Cardinale, M., Rayner, D.,
26
27 352 Wennhage, H., Casini, M. (2014) Predicting fish stock dynamics under climate change: Baltic
28
29 353 herring as a case study. *Fisheries Oceanography* 23:258–269.

30
31
32 354 Batten, S.D., Clarke, R., Flinkman, J., Hays, G., John, E., John, A.W.G., Jonas, T.D., Lindley, J.A.,
33
34 355 Stevens, D., and Walne, A. (2003) CPR sampling: the technical background, materials and methods,
35
36 356 and issues of consistency and comparability. *Progress in Oceanography* 58:193-215.

37
38
39
40 357 Engelhard, G. H., Peck, M. A., Rindorf, A., Baumgartner, T., Soutar, A., and Ferreira-Bartrina, V.
41
42 358 (1992) Reconstruction of the history of Pacific sardine and northern anchovy populations over the
43
44 359 past two millennia from sediments of the Santa Barbara basin. *CalCOFI Rep.* 33:24–40.

45
46
47 360 Berntsen, J., Skagen, D. W., and Svendsen, E. (1994). Modelling the transport of particles in the
48
49 361 North Sea with reference to sandeel larvae. *Fisheries Oceanography* 3:81-91.

1
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5
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7
8
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11
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14
15
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51
52
53
54
55
56
57
58
59
60

362 Beare, D., Burns, F., Jones, E., Peach, K., Portilla, E., Greig, T., ... and Reid, D. (2004) An increase
363 in the abundance of anchovies and sardines in the north-western North Sea since 1995. *Global*
364 *Change Biology* 10:1209-1213.

365 Beaugrand, G. (2004) The North Sea regime shift: evidence, causes, mechanisms and
366 consequences. *Progress in Oceanography* 60:245-262.

367 Coetzee, J. C., van der Lingen, C. D., Hutchings, L., and Fairweather, T. P. (2008) Has the fishery
368 contributed to a major shift in the distribution of South African sardine? *ICES Journal of Marine*
369 *Science* 65:1676–1688.

370 Checkley, D.M., Alheit, J., and Oozeki, Y. (Editors) (2009) Climate change and small pelagic fish.
371 Cambridge University Press, Cambridge.

372 Checkley, D.M., Asch, R., Rykaczewski, R. (2017). Climate, Anchovy, and Sardine. *Annual Review*
373 *of Marine Science* 9:469–93.

374 Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J., and Verheye,
375 H.M. (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in
376 “wasp-waist” ecosystems. *ICES J. Mar. Syst.* 57:603–618.

377 Dickey-Collas, M., Engelhard, G. H., Rindorf, A., Raab, K., Smout, S., Aarts, G, Garthe, S. (2013)
378 Ecosystem-based management objectives for the North Sea: riding the forage fish
379 rollercoaster. *ICES Journal of Marine Science* 71:128-142.

380 Dragesund O., Hamre J., and Ulltang Ø (1980) Biology and population dynamics of the Norwegian
381 spring-spawning herring. *Rapports et Procès-Verbaux des Réunions du Conseil International pour*
382 *l'Exploration de la Mer* 177:43-71.

- 383 Eigaard, O. R., Deurs, M. V., Behrens, J., Bekkevold, D., Brander, K., Plambech, M., and
384 Mosegaard, H. (2014) Prey or predator—expanding the food web role of sandeel (*Ammodytes*
385 *marinus*). *Marine Ecology Progress Series* 516:267-273.
- 386 Eliassen, K., Reinert, J., Gaard, E., Hansen, B., Jacobsen, J. A., Grønkjær, P., and Christensen, J. T.
387 (2011) Sandeel as a link between primary production and higher trophic levels on the Faroe
388 shelf. *Marine Ecology Progress Series* 438:185-194.
- 389 Engelhard, G. H., Peck, M. A., Rindorf, A., Smout, S. C., van Deurs, M., Raab, K., and Brunel, T.
390 (2014) Forage fish, their fisheries, and their predators: who drives whom? *ICES Journal of Marine*
391 *Science* 71: 90-104.
- 392 Fishbase (2016) http://www.aquamaps.org/receive.php?type_of_map=regular
- 393 Frederiksen, M., Furness, R. W., and Wanless, S. (2007) Regional variation in the role of bottom-up
394 and top-down processes in controlling sandeel abundance in the North Sea. *Marine Ecology*
395 *Progress Series* 337:279-286.
- 396 Fréon, P., Bouchon, M., Mullon, C., García, C., and Ñiquen, M. (2008) Interdecadal variability of
397 anchoveta abundance and overcapacity of the fishery in Peru. *Prog. Oceanogr.* 79: 401–412.
- 398 Furness, R. W., & Tasker, M. L. (2000) Seabird-fishery interactions: quantifying the sensitivity of
399 seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in
400 the North Sea. *Marine Ecology Progress Series* 202:253-264.
- 401 Greenstreet, S. P., Armstrong, E., Mosegaard, H., Jensen, H., Gibb, I. M., Fraser, H. M. and
402 Sharples, J. (2006) Variation in the abundance of sandeels *Ammodytes marinus* off southeast
403 Scotland: an evaluation of area-closure fisheries management and stock abundance assessment
404 methods. *ICES Journal of Marine Science* 63:1530-1550.

1
2
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6
7
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10
11
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14
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42
43
44
45
46
47
48
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50
51
52
53
54
55
56
57
58
59
60

405 Gårdmark A., Lindegren, M., Neuenfeldt, S., Blenckner, T., Heikinheimo, O., Müller-Karulis, B.,
406 Niiranen, S., Tomczak, M., Aro, E., Wikström, A., Möllmann, C. (2013). Biological ensemble
407 modelling to evaluate potential futures of living marine resources. *Ecological Applications*, 23:742–
408 754.

409 Hastie, T., and Tibshirani, R. (1990) Generalized additive models. Chapman and Hall, London.

410 Helaouët, P., and Beaugrand, G. (2007) Macroecology of *Calanus finmarchicus* and *C.*
411 *helgolandicus* in the North Atlantic Ocean and adjacent seas. *Marine Ecology Progress*
412 *Series* 345:147-165.

413 Hjermann, D.O., Ottersen, G., and Stenseth, N.C. (2004) Competition among fishermen and fish
414 causes the collapse of Barents Sea capelin. *Proc. Natl. Acad. Sci. U.S.A.* 101:11679–11684.

415 ICES (2017) Report of the Benchmark on Sandeel (WKSand 2016), 31 October - 4 November
416 2016, Bergen, Norway. ICES CM 2016/ACOM:33. 301pp.

417 Jansen, T., and Gislason, H. (2011) Temperature affects the timing of spawning and migration of
418 North Sea mackerel. *Continental Shelf Research* 31:64-72.

419 Jensen, H., Rindorf, A., Wright, P. J., and Mosegaard, H. (2010) Inferring the location and scale of
420 mixing between habitat areas of lesser sandeel through information from the fishery. *ICES Journal*
421 *of Marine Science* 68:43-51.

422 Jónasdóttir, S. H., and Koski, M. (2011) Biological processes in the North Sea: comparison of
423 *Calanus helgolandicus* and *Calanus finmarchicus* vertical distribution and production. *Journal of*
424 *Plankton Research* 33:85-103.

- 425 Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., and Roy, C.
426 (2006) Climate variability, fish, and fisheries. *Journal of Climate* 19:5009-5030.
- 427 Lindegren M., C. Möllmann, A. Nielsen, K. Brander, B. R. MacKenzie, and Stenseth N. C. (2010)
428 Ecological forecasting under climate change: the case of Baltic cod. *Proceedings of the Royal*
429 *Society B-Biological Sciences* 277:2121-2130.
- 430 Lindegren, M., Östman, Ö., and Gårdmark, A. (2011) Interacting trophic forcing and the population
431 dynamics of herring. *Ecology* 92:1407–1413.
- 432 Lindegren M., Blenckner T., and Stenseth N. C. (2012) Nutrient reduction and climate change cause
433 a potential shift from pelagic to benthic pathways in a eutrophic marine ecosystem. *Global Change*
434 *Biology* 18:3491-3503.
- 435 Lindegren, M., and D.M. Checkley, Jr. (2013) Temperature dependence of Pacific sardine
436 (*Sardinops sagax*) recruitment in the California Current revisited and revised. *Canadian Journal of*
437 *Fisheries and Aquatic Sciences* 52:566-577.
- 438 Lindegren, M., Checkley Jr. D. M., Rouyer T., MacCall A. D., and Stenseth N. C. (2013) Climate,
439 fishing, and fluctuations of sardine and anchovy in the California Current. *Proceedings of the*
440 *National Academy of Sciences of the United States of America* 110:13672-13677.
- 441 Lindegren, M., Checkley, D.M., Jr., Ohman, M.D., Koslow, A., Goericke, R. (2016). Resilience and
442 Stability of a Pelagic Marine Ecosystem. *Proceedings of the Royal Society B-Biological Sciences*
443 283:20151931.
- 444 Long, R.D., Charles, A., Stephenson, R.L. (2015) Key principles of marine ecosystem-based
445 management. *Marine Policy* 57:53-60.

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47
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54
55
56
57
58
59
60

446 Lynam, C. P., Halliday, N. C., Höffle, H., Wright, P. J., van Damme, C. J., Edwards, M., and Pitois,
447 S. G. (2013) Spatial patterns and trends in abundance of larval sandeels in the North Sea: 1950–
448 2005. *ICES Journal of Marine Science* 70:540-553.

449 Macer, C. T. (1966) Sandeels (Ammodytidae) in the south-western North Sea: Their biology and
450 fishery. *MAFF Fishery Invest, London ser.* 1-55 pp. MacKenzie, B.R., Meier, H.E.M., Lindegren,
451 M., Neuenfeldt, S., Eero, M., Blenckner, T., Tomczak, M.T., and Niiranen, S. (2012) Impact of
452 climate change on fish population dynamics in the Baltic Sea: A dynamical downscaling
453 investigation. *Ambio* 41: 626-636.

454 McLeod, K. and Leslie H. (2009) Ecosystem-based management for the oceans. Island Press,
455 Washington, D.C., USA.

456 Möllmann C., Diekmann R., Müller-Karulis B., Kornilovs G., Plikshs M., and Axe P. (2009)
457 Reorganization of a large marine ecosystem due to atmospheric and anthropogenic pressure: a
458 discontinuous regime shift in the Central Baltic Sea. *Glob Change Biol* 15:1377–1399.

459 Myers, R. A. (1998) When do environment–recruitment correlations work?. *Reviews in Fish*
460 *Biology and Fisheries* 8: 285-305.”

461 Pankhurst, N. W., and Munday, P. L. (2011) Effects of climate change on fish reproduction and
462 early life history stages. *Marine and Freshwater Research* 62:1015-1026.

463 Picard, R.R., and Cook, R.D. (1984) Cross-validation of regression models. *J. Am. Stat. Assoc.*
464 79:575–583.

465 Pershing, A. J., et al. (2015). Slow adaptation in the face of rapid warming leads to collapse of the
466 Gulf of Maine cod fishery. *Science* 350: 809-812.

- 1
2
3
4 467 Petitgas, P., Alheit, J., Peck, M. A., Raab, K., Irigoien, X., Huret, M., ... and Dickey-Collas, M.
5
6 468 (2012) Anchovy population expansion in the North Sea. *Marine Ecology-progress Series* 444:1-13.
7
8
9 469 Pitois, S. G., and Fox, C. J. (2006) Long-term changes in zooplankton biomass concentration and
10
11 470 mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data.
12
13 471 ICES Journal of Marine Science 63: 785-798.
14
15
16
17 472 Pörtner, H.O. (2002) Climate variations and the physiological basis of temperature dependent
18
19 473 biogeography: Systemic to molecular hierarchy of thermal tolerance in animals. *Comparative*
20
21 474 *Biochemistry and Physiology - A Molecular and Integrative Physiology* 132:739–761.
22
23
24 475 Raab, K., Nagelkerke, L. A. J., Boérée, C., Rijnsdorp, A. D., Temming, A., and Dickey-Collas, M.
25
26 476 (2012) Dietary overlap between the potential competitors herring, sprat and anchovy in the North
27
28 477 Sea. *Marine Ecology Progress Series* 470:101-111.
29
30
31 478 Reid, P. C., Edwards, M., Hunt, H. G., and Warner, A. J. (1998) Phytoplankton change in the North
32
33 479 Atlantic. *Nature* 391:546-546.
34
35
36
37 480 Richardson, K., Jónasdóttir, S. H., Hay, S. J., and Christoffersen, A. (1999) *Calanus finmarchicus*
38
39 481 egg production and food availability in the Faroe–Shetland Channel and northern North Sea:
40
41 482 October–March. *Fisheries Oceanography* 8:153-162.
42
43
44 483 Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M.,
45
46 484 Fletcher, W.J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S.E.,
47
48 485 Maccall, A.D., Matsuura, Y., Nevarez-Martinez, M.O., Parrish, R.H., Roy, C., Serra, R., Shust,
49
50 486 K.V., Ward, M.N., and Zuzunaga, J.Z. (1999) Worldwide large-scale fluctuations of sardine and
51
52 487 anchovy populations. *S. Afr. J. Mar. Sci.* 21:289–347.
53
54
55
56
57
58
59
60

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3
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5
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53
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55
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57
58
59
60

488 Skern-Mauritzen, M., Ottersen, G., Handegard, N. O., Huse, G., Dingsør, G. E., Stenseth, N. C. and
489 Kjesbu, O. S. (2016) Ecosystem processes are rarely included in tactical fisheries management. *Fish*
490 *and Fisheries* 17: 165–175.

491 Steele, J. H. and Henderson, E. W. (1984) Modelling long-term fluctuations in fish stocks. *Science*
492 224:985–987.

493 Johns D. (2017) Monthly averaged zooplankton data for sandeel management area 1 1958-2015 as
494 recorded by the Continuous Plankton recorder, Sir Alister Hardy Foundation for Ocean Science.
495 Plymouth. [25/05/2017] DOI is 10.7487/2017.178.1.1061.

496 Van der Lingen C.D., Hutchings L., and Field J.G. (2006) Comparative trophodynamics of anchovy
497 *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: Are species
498 alternations between small pelagic fish trophodynamically mediated? *Afr J Mar Sci* 28:465–477.

499 Van Deurs, M., van Hal, R., Tomczak, M. T., Jónasdóttir, S. H., and Dolmer, P. (2009).
500 Recruitment of lesser sandeel *Ammodytes marinus* in relation to density dependence and
501 zooplankton composition. *Marine ecology progress series* 381:249-258.

502 Van Deurs, M., Hartvig, M., and Steffensen, J. F. (2011) Critical threshold size for overwintering
503 sandeels (*Ammodytes marinus*). *Marine biology* 158:2755-2764.

504 Van Deurs, M., Koski, M., and Rindorf, A. (2014) Does copepod size determine food consumption
505 of particulate feeding fish?. *ICES Journal of Marine Science* 71:35-43.

506 Van Deurs, M., Jørgensen, C., and Fiksen, Ø. (2015) Effects of copepod size on fish growth: a
507 model based on data for North Sea sandeel. *Marine Ecology Progress Series* 520:235-243.

- 508 Van Deurs, M., Christensen, A., and Rindorf, A. (2013) Patchy zooplankton grazing and high
509 energy conversion efficiency: ecological implications of sandeel behavior and strategy. *Marine*
510 *Ecology-Progress Series* 487:123-133.
- 511 Wood, S.N. (2006) Generalized additive models. An introduction to R. Chapman & Hall/CRC,
512 Boca Raton.
- 513 Wright, P. J., and Bailey, M. C. (1996) Timing of hatching in *Ammodytes marinus* from Shetland
514 waters and its significance to early growth and survivorship. *Marine Biology* 126:143-152.
- 515 Wright, P. J., Jensen, H., and Tuck, I. (2000) The influence of sediment type on the distribution of
516 the lesser sandeel, *Ammodytes marinus*. *Journal of Sea Research* 44:243-256.
- 517 Wright, P. J., Jensen, H., and Tuck, I. (2000) The influence of sediment type on the distribution of
518 the lesser sandeel, *Ammodytes marinus*. *Journal of Sea Research* 44: 243–256.

TABLES

Table 1. Information about the abiotic and biotic covariates used during model fitting with regards to spatial and temporal coverage, as well as the source of dataae.

Variable	Month	Area	Data source
SSTQ1	Jan-March	Dogger Bank	http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html
SSTQ2	April-June	Dogger Bank	http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html
SSTQ3	July-Sept	Dogger Bank	http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html
SSTQ4	Oct-Dec	Dogger Bank	http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html
SST Annual	Jan-Dec	Dogger Bank	http://www.metoffice.gov.uk/hadobs/hadisst/data/download.html
SBT Annual	Jan-Dec	North Sea	http://ecosystemdata.ices.dk/
NAO Annual	Jan-Dec	North Atlantic	https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based
<i>C.finmarchicus</i>	Jan-Dec	Dogger Bank	Johns (2017)
<i>T.longicornis</i>	Jan-Dec	Dogger Bank	Johns (2017)

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 $\text{edf} > 1$ 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 are recruitment success and juvenile survival are represented by (c) mean sea surface temperatures (SST) and the abundance of *C. finmarhicus* 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

SSB (solid), abundance at age 1 (dashed) and temperature (dotted) on sandeel recruitment success when successively fitting and annually updating the final model on data from 1997 to 2015. (The horizontal gray dashed line indicate significance at $p=0.05$).

Figure 5. (a) Hindcast simulations of sandeel SSB based on: (i) observed SST, *C. finmarchicus*, *T. longicornis* and F values (black); (ii) reduced F to current levels (2010-2015) (black dashed); (iii) reduced SST to mean levels during the 1980s (black dotted); (iv) introduced peaks in *C. finmarchicus* in 1998, 2001, 2004 and 2007 (grey solid); (v) and all changes (ii-iv) together (grey dashed). The solid horizontal red line marks the limiting stock level (B_{lim}). (b) Probability of SSB falling below B_{lim} given changes in mean SST (by -1 to 2°C) and fishing, given by a scaling factor on mean fishing mortalities-at-age (F multiplier) ranging from 0 to 2, hence representing a fishing closure and doubling of mean F, respectively (where 1 represent F equal to the long-term average, $F_{age1-2} = 0.71$).

Figure 1

218x209mm (72 x 72 DPI)

Figure 2

185x212mm (72 x 72 DPI)

Figure 3

161x203mm (72 x 72 DPI)

Figure 4

187x217mm (72 x 72 DPI)

Figure 5

254x190mm (96 x 96 DPI)

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
SSTQ2	0.411	66.7
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.

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 polynomium $\ln(R/S) = c_1 \ln(S) + c_2 \ln(S)^2 + c_3 \ln(N) + c_4 \ln(N)^2 + c_5T + c_6Z_1 + c_7Z_2 + k$ (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), Z₁ (CPR index for *Calanus finmarchicus*), and Z₂ (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 (c₁ – c₇ 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.