The factors driving the spatiotemporal population dynamics of sandeel in the North Sea

Henriksen, Ole

Publication date: 2020

Document Version
Publisher's PDF, also known as Version of record

Citation (APA):
Henriksen, O. (2020). The factors driving the spatiotemporal population dynamics of sandeel in the North Sea. DTU Aqua.
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Ole Henriksen
PhD Thesis
2020
The factors driving the spatiotemporal population dynamics of sandeel in the North Sea

PhD Thesis

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Section for Marine Living Resources
National Institute of Aquatic Resources (DTU AQUA)
Technical University of Denmark (DTU)

Academic dissertation
To be defended May 7, 2020, at Technical University of Denmark, Kgs. Lyngby, Denmark

Submission:
February 28, 2020

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1. Preface
Submitted in fulfilment of requirements for Doctor of Philosophy Degree (PhD) at the Technical University of Denmark (DTU). This thesis is structured as literature review, constituting the synthesis, and four individual studies (Paper in roman numerals I-IV). The research presented in the thesis was carried out at the Section for Marine Living Resources under the National Institute for Aquatic Resources (DTU Aqua) between February 2017 and February 2020 under supervision by Dr. Mikael van Deurs, Prof. Henrik Mosegaard, and Dr. Asbjørn Christensen. The PhD was funded by European Maritime and Fisheries Foundation & Ministry of Environment and Food under grant agreement Denmark (grant ID: 33113-B-16-080; project: Management plans for fish stocks) and DTU Aqua PhD school. Additional funding for external stays, coursework, and participation in conferences was received from the Otto Mønsted Fond.

“To cope alone and unaided with a subject so vast, so complex, and so infinitely mysterious as the sea would be a task not only cheerless but impossible, and I have not attempted it.”

Rachel L. Carson, The Sea Around Us, 1951.
### 1.2 List of publications presented in thesis

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<th>Title</th>
<th>Journal</th>
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<td>Henriksen, O., Rindorf, A., Brooks, M. E., Lindegren, M., &amp; van Deurs, M. (in prep.).</td>
<td>Temperature and body size affect recruitment and survival of sandeel across the North Sea</td>
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<tr>
<td>Paper IV</td>
<td>Henriksen, O., Rindorf, A., Payne, M., Mosegaard, H., &amp; van Deurs, M. (in prep.).</td>
<td>Get up early: climate change leads to behavioral changes in sandeel.</td>
<td></td>
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1.3 Other publications during PhD


1.4 Conference presentations during PhD


1.5 ICES working groups during PhD

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<td>ICES, Copenhagen, Denmark</td>
<td>2017</td>
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<tr>
<td>Herring Assessment Working Group for the Area South of 62° N (HAWG)</td>
<td>ICES, Copenhagen, Denmark</td>
<td>2018</td>
</tr>
<tr>
<td>Working Group on Seasonal-to-Decadal Prediction of Marine Ecosystems (WGS2D)</td>
<td>ICES, Copenhagen, Denmark</td>
<td>2018</td>
</tr>
<tr>
<td>Herring Assessment Working Group for the Area South of 62° N (HAWG)</td>
<td>ICES, Copenhagen, Denmark</td>
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<td>Herring Assessment Working Group for the Area South of 62° N (HAWG)</td>
<td>ICES, Copenhagen, Denmark</td>
<td>2020</td>
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1.6 External stay during PhD

Ongoing collaboration with Espen Johnsen on projects that investigates the current management of sandeel in Norwegian waters. Participated in the acoustic survey for sandeel. *Institute of Marine Research, Bergen, 2018, 2019*
1.7 Acknowledgements
This thesis is the product of invaluable help and collaboration from numerous people and institutions, and to those I may forget here – Thank You.

First and foremost, I would like to thank my supervisors Mikael van Deurs, Henrik Mosegaard and Asbjørn Christensen for presenting this opportunity to conduct amazing and exiting research. A special thanks go to Mikael; for sharing knowledge, for continuous guidance and support, for the enormous trust in my independence, for always taking the time necessary to answer questions, and for supporting my journey and presence in research for years to come; to Henrik for interesting scientific discussions and guidance; to Anna Rindorf for inspirational presence, scientific work and career advice. I would also like to express a special thanks to all the other co-authors; Martin, Mollie, Mark, Sigrun, Brian, Kristian.

“I have yet much to learn”

Throughout my PhD at DTU Aqua, I have been fortunate to be part of a fantastic group of colleagues; Marie, thank you for the cheering, positive vibes, deep conversations and for being a wonderful friend; Tobias, my desk neighbour, thank you for supporting me during the long nights; Gitte, thank you for the money. Other I need to mention; Aurore; Ciaran, Søren, Marie, Tim, Tommy, Jane, Peter and Kristian, I am grateful having had such cheerful and talented colleagues.

I also had the privilege to collaborate with Espen Johnsen from Institute of Marine Research during my studies in Bergen and participation in a scientific survey. Thanks, and I am excited to continue our ongoing scientific work together.

The financial support by DTU Aqua PhD school and the European Maritime and Fisheries Foundation & Ministry of Environment and Food under grant agreement Denmark (grant ID: 33113-B-16-080; project: Management plans for fish stocks) to conduct the research described in this thesis and supported papers is greatly acknowledged.

Gratitude also goes out to friends and family for the support.

Finally, but never to forget, I am deeply grateful to my two daughters, Pil and Svea, and you - Maja. Words can never express how deeply grateful I am - Thanks, for the unconditional support, patience and time/space when science steal our time. Thank you for being a wonderful mother and best friend - I love you.

Ole Henriksen, 2020
1.8 Summary
Trophic levels in “wasp-waist” systems are characterized by an intermediate level that are occupied by a few highly abundant schooling planktivorous species, also termed forage fish. The flow of energy in the food webs are channelled from a species-rich lower trophic level of plankton through forage fish to higher trophic levels of a diverse predator community. The abundance of forage fish fluctuates and thus, ecosystems can be highly sensitive to changes in populations dynamics of these species. While the impact on the ecosystem have been well documented, the underlying processes and mechanisms behind are still vaguely understood.

In the North Sea, the majority of forage fish are small pelagic fish that migrate between areas of foraging and spawning. Yet, sandeel (*Ammodytes marinus*) represent a forage fish with a completely different life history, which include a specialized burying strategy that links this species to a specific habitat making them highly site-attached and patchy in distribution. As a consequence of these life history traits, sandeels are vulnerable to changes in environment, demographic processes, and exploitation. They play a major role in the diet of seabirds, marine mammals and predatory fish, as well as being one of the largest single species fisheries in the North Sea. Hence, knowledge about what drives the population dynamics are essential for conservation and sustainable exploitation of this species, which support important ecosystem services, including biodiversity and human livelihoods.

This thesis consist of four individual studies (Paper I to IV) and a literature review, constituting the synthesis. The review was conducted in order to provide an overview of current knowledge about important factors that drive the population dynamics of sandeel in the North Sea. Presented in this thesis, are sections on growth, density dependence, habitat, food availability, predation, fisheries, temperature, oceanography and broad-scale climate. Additional explorative analyses were made, when applicable, providing supporting information to aid interpretations and facilitate discussion. Findings from the four studies, representing three years of research, are highlighted in boxes (see Box overviews) throughout the thesis, where they serve to fill in knowledge gaps on the effect of oceanography (Paper I), density dependence (Paper II) and temperature (Paper III and Paper IV).
1.9 Resumé (Dansk)

Trofiske niveauer i "hvepse-talje"-systemer (også kendt som "timeglas"-system) er kendtegnet ved et mellemniveau, der er besat af nogle ganske få meget talrige arter af stimefisk, der også betegnes som byttefisk, skidtfisk eller foderfisk. Energistrømmen igennem fødenettet kanaliseres fra et artsrigt lavere trofisk niveau af plankton gennem byttefisk til de højere trofiske niveauer bestående af top-prædatorer. Mængden af byttefisk har store udsving og økosystemer kan således være meget følsomme over for ændringer i bestandsdynamikken hos disse arter. Effekten af disse udsving på økosystemet er veldokumenteret, men viden om de bagvedliggende processer og mekanismer er mangelfuld.


Denne afhandling forsøger at give et overblik over den aktuelle viden om vigtige faktorer, der driver bestandsdynamikken for tobis i Nordsøen. En gennemgang af litteraturen gjorde det muligt at identificere de vigtigste faktorer, der har indflydelse på tobisforekomsten. I afhandlingen diskuteres afsnit om vækst, bestandstætheder, habitat, føde, prædation, fiskeri, temperatur, oceanografi og vejrfænomener i bred skala. Derudover bruges undersøgende analyser som baggrund for fortolkninger og diskussioner. Endvidere fremhæves ny forskning i fire artikler der undersøger effekten af oceanografi (*Paper I*), tæthedseffekter (*Paper II*) og temperatur (*Paper III* og *Paper IV*) flere steder i afhandlingen (Se tekstboks, *Box overviews*).

Disse artikler gengiver vigtige fund fra tre års forskning, der tilvejebringer væsentlig viden om forståelsen af vigtige mekanismer, der påvirker den tidlige livfase (dvs. rekruttering) og voksenalderen (dvs. biomassen den er tilgængelig for fiskeri).
2. Introduction
The role of bottom-up (i.e. resource-limited) and top-down (i.e. predation-controlled) processes is a central theme in ecology (Wollrab et al., 2012; Young et al., 2015; Lynam et al., 2017) and is fundamental to understanding how factors affect ecosystem dynamics. Highly diverse lower and upper trophic levels, and a less diverse intermediate level characterize marine ecosystems on continental shelves (Bakun, 2006; Fauchald et al., 2011). Such a system has been coined a “wasp-waist” system (Cury, 2000), where the intermediate levels are occupied by a few highly abundant schooling species, which are fast-growing, short-lived and planktivorous, having the capacity to exert top-down grazing on zooplankton and bottom-up regulation on top predators. Forage fish often represent this mid-trophic link in the food web (Hilborn et al., 2017). Since energy transfer happens from species-rich lower trophic levels through a few highly abundant species that dominate the intermediate trophic level, ecosystem functions and services (e.g. food for higher trophic levels including natural predators and humans) are highly sensitive to fluctuations and availability of these species (Yaragina and Dolgov, 2009; Schindler et al., 2010; Vert-Pre et al., 2013; Dickey-Collas et al., 2014).

The group that constitutes forage fish in the North Sea includes mainly clupeiform fishes (herring Clupea harengus, sprat Sprattus sprattus, sardine Sardina pilchardus and anchovy Engraulis encrasicolus), typically mobile, small pelagic fish that migrate between foraging and spawning grounds (Fauchald et al., 2011; Engelhard et al., 2014). Unlike other forage fish, sandeel (also Raitt’s sandeel Ammodytes marinus) is a highly resident and non-migratory fish that also fulfils a similar role in the North Sea. In fact, sandeel has been highlighted as the most important forage fish in the North Sea, because it constitutes the major food source for many predatory fish, seabirds and marine mammals (Greenstreet et al., 1998; Furness, 2002; Heath et al., 2009; Engelhard et al., 2014). In recent years, the largest single species fishery in the North Sea has been industrial fishing for sandeel (Dickey-Collas et al., 2014), and from a global perspective it has been the seventh-largest commercially targeted stock ever reported (Checkley et al. 2010). Thus, the availability of sandeel to the North Sea ecosystem has a great impact on prey and predators, including fisheries.

The recruitment of sandeel has dramatic interannual fluctuations, with a large year-class typically being followed by a small one; and occasionally, an unusually strong year-class can sustain large biomasses for several years (ICES, 2018). The variability in recruitment also affects the available biomass of older fish over time, and current knowledge indicates that sandeel, as well as clupeids (McClatchie et al., 2017), have “boom-and-bust” cycles of high
and low productivity (Clausen et al., 2017). Since the early 2000s, the stock biomass has rapidly declined, together with the landings and profitability of the fishery (Dickey-Collas et al., 2014; ICES, 2018; Lindegren et al., 2018). Consequently, two decades’ worth of quota regulations have been put in place to promote stock recovery (ICES, 2010), yet stock biomass has since remained at low levels. Environmental forcing has been highlighted as the main driver of such population dynamics (Szuwalski and Hilborn, 2015). Nevertheless, several factors have been proposed as driving the population dynamics of sandeel, including intrinsic factors such as density dependence (Arnott and Ruxton, 2002; van Deurs et al., 2009; Lindegren et al., 2018) and growth (Eliasen et al., 2011; Clausen et al., 2017), as well as several extrinsic factors of climate forcing, fishing (Frederiksen et al., 2004; Lindegren et al., 2018) and predation (Greenstreet et al., 1998; Engelhard et al., 2014; Reilly et al., 2014).

Sandeel have specialized life history characteristics, such as high site fidelity, burying behaviour and winter dormancy (i.e. overwintering), which limits distribution in time and space (Wright et al., 2000; Jensen et al., 2011; van Deurs et al., 2011). These features complicate the dynamics and have a profound impact on the availability of sandeel in the ecosystem. The availability of adult sandeel is largely confined to the seasonal timing of the springtime growth period, when they resurface after overwintering to forage on copepods (Reeves, 1994; van Deurs et al., 2013). Furthermore, the timing of specific life history events is assumed to be important for the survival of early life stages, when hatching and settlement are assumed to be associated with food availability (Régnier et al., 2017, 2019; MacDonald et al., 2019a) and oceanographic features (Christensen et al., 2008; Gurkan et al., 2013). Therefore, a knowledge of what influences important life history events through time and space is important in order to understand what may impact the biology of sandeel.

This thesis synthesizes the current understanding of factors driving the population dynamics of sandeel populations in the North Sea while highlighting previous, ongoing and future research. The synthesis begins by outlining the life cycle and important life history events which set the scene and provide a basic biological knowledge essential for understanding the population dynamics. Reviewing the literature enables important driving factors for sandeel abundance to be pinpointed. Findings from three years of research are highlighted and put into context for relevant sections (see Box overview). Available stock-recruit data provide a solid background for understanding mechanisms and dynamics. The data provides an opportunity to do explorative data analysis (see Materials and methods) when needed, to shed light on important aspects that drive fluctuations in sandeel population.
parameters. Insights from these investigations enable us to more elaborately interpret and discuss some of the evidence of intrinsic and extrinsic factors that are important drivers for the sandeel in the North Sea found in the literature.

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**Box overviews**

This thesis covers the findings from the following papers:

1. Specific flow regimes in February coincide with extreme years of recruitment. The flow regimes in February perform better than other environmental predictors in explaining extreme recruitment ([Paper I](#), Henriksen et al. 2018, *Oceanographic flow regime and fish recruitment: reversed circulation in the North Sea coincides with unusually strong sandeel recruitment*).

2. Density-dependent effects in sandeel are dependent on spatial scales. Two types of local density-dependent processes were identified, where both distribution shifts and density increases were evident, but the processes seemed to largely compensate for each other on a regional scale ([Paper II](#), Rindorf et al. 2019, *Scale-specific density dependence in North Sea sandeel*).

3. Important intrinsic and extrinsic factors influenced the first two years of life. Length at age was found to be the only factor influencing sandeel abundances during the first year of life. During the second year temperature was found to impact sandeel while accounting for cohort effects. Spatial temperature had a stronger impact in southern areas of the North Sea ([Paper III](#), Henriksen et al., in prep., *Temperature and body size affect recruitment and survival of sandeel across the North Sea*).

4. Warm years correlated with the earlier emergence of sandeel after their specialized overwintering phase. Using a model that describes the bioenergetics made it possible to give a plausible explanation of the underlying mechanisms. ([Paper IV](#), Henriksen et al., in prep., *Get up early: climate change leads to behavioural changes in sandeel*).

Short highlights and summaries of these papers are given in communication boxes. Boxes are shown throughout the synthesis in relevant sections.
3. Materials and methods

Available data from a recent stock assessment model (Lewy and Vinther, 2004; ICES, 2018) based on current management areas (i.e. SA1, SA2, SA3 and SA4, see ICES (2016)) was used to present historical trends and explorative analyses in different sections of the thesis. The variation between areas was investigated via a series of linear models (LM in tables). Furthermore, linear mixed models (LMM in tables) were used to detect predictor effects that might be common to a combined North Sea on a regional scale. The spatial division of the four management areas was included as a random effect. Model formulations are comparable to previous work on sandeel (Arnott and Ruxton, 2002; van Deurs et al., 2008, 2009; Lindegren et al., 2018), but see also Paper III for more detailed information). The data includes recruitment (R) as a proxy for early life, spawning stock biomass (SSB) as a proxy for adults and sometimes recruitment success (R/SSB) as a proxy for productivity. Where available and applicable, a set of intrinsic and extrinsic factors was chosen to present historical trends and/or explorative model analysis to aid in the interpretation and discussion of each driving factor (Table 1). These factors were identified based on a review of current literature.


<table>
<thead>
<tr>
<th>Classification</th>
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<th>Explanation</th>
<th>Data</th>
<th>Thesis section</th>
<th>Application</th>
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<td>R</td>
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4. The availability of sandeel to the North Sea ecosystem

The availability of sandeel to the ecosystem depends chiefly on the main periods of the life cycle. The life cycle includes important life history events that have great impacts on the time and place of abundances. Accordingly, the measure of abundance can be described on a spatial and temporal continuum. The time and place of observations informs the potential environmental variability that may affect sandeel abundances. These measures are not mutually exclusive, as both time and space influence the magnitude of the observation signal for available abundances. Hence, the availability of sandeel to the ecosystem can be defined by the life cycle associated with important life history events through time and space that defines the magnitude of abundances.
4.1 Life cycle
The life cycle includes several important ontogenetic phases (Fig. 1). In short, ontogenetic development can be divided into 1) early life and 2) adults. Early life (i.e. egg and larvae) is concentrated within the first critical months of life before metamorphosis and settlement (Macer, 1966; Wright and Bailey, 1996). Sandeel hatch from eggs attached to sand grains and begin a short larval drift phase before later developing active swimming and juvenile schooling behaviour (Monteleone and Peterson, 1986; Proctor et al., 1998). They metamorphose at a length of ~45 mm, whereafter they settle into sandy habitats in early summer, joining the adult segment of the population. Once settled, the juveniles (or young adults) adhere to adult behaviour, but spawning behaviour is expected to happen at the end of the second year of life at the earliest (Gauld and Hutcheon, 1990; Boulcott et al., 2007). Due to high site fidelity for post-settled sandeel, adult sandeel are expected to be closely linked to a patchwork of sandbanks with little exchange between them (Wright et al., 2000; Holland et al., 2005; Jensen et al., 2011).

Figure 1. Illustration of the life cycle of sandeel. Early life is depicted by white arrows, the shift to adult behaviour associated with settlement by a grey arrow and adults by black arrows.
4.2 Timing of life history events

The timing of recurring life history events and how they are influenced by environmental variability is a major driver of the population dynamics of sandeel. These events are closely bound to ontogenetic development. Here, the development that contributes to early life is very different from the development after joining the adult population.

![Diagram of life history events](image)

**Figure 2.** Illustration of the important life history events of sandeel. The annual shape of abundance curves expected in early life and adults is also shown. Hatching and settlement are highlighted for early life (upper panel), and periods of feeding and overwintering are highlighted for adults (lower panel). Spawning happens in Dec/Jan.

Early life is clumped into approximately 3–6 critical months, during which recruitment (i.e. year-class strength) is believed to be established between key timing events of hatching and settlement (Fig. 2, **Box 1**). Thus, early life development provides several vectors – from egg through larval drift to settled juvenile (Christensen *et al.*, 2008) – for environmental drivers to influence abundance. The abundances are then expected to decrease during pelagic larval drift until settlement due to high mortality rates among early life stages.
Abundances of adult sandeel are largely affected by seasonal behaviour, which includes phases of burying and feeding (Fig. 2). Adult individuals have two main seasonal phases: feeding and overwintering (van Deurs et al., 2010, 2013). These abundances are hypothesized to follow a dome-shaped curve (Reeves, 1994), where the abundance of adult sandeel gradually increases as sandeel emerge from overwintering until feeding activity reaches a peak and then decreases (Box 2). During spring, they emerge from the sand and begin foraging, made up of diel behaviour alternating between the upper pelagic zone, forming large schools during daylight to feed on zooplankton and burying themselves in sediment at night (Winslade, 1974a; Freeman et al., 2004). The overwintering period includes a specialized behaviour comprising a strategy that involves burial in sandy sediment, surviving on energy reserves obtained during the feeding season (Wright et al., 2017a; MacDonald et al., 2018). The exact overwintering period is not well-described, but based on decreasing fishery catches it presumably lasts for approximately 8 months on average between August and April, interrupted only by spawning around December/January (maturation from ages ~1-3).
Spatially, abundances of sandeel are closely coupled with the annual timing of these events.

Box 2. Highlight from Paper IV: Catches reflects life history event in sandeel

Henriksen et al. (in prep.)

Data that describe important life history events are often unavailable. However, previous findings seem to indicate that commercial catch data may describe the timing associated with seasonal emergence of sandeel from overwintering. These assumption make it possible to develop methods for estimating and describing an essential life history event of sandeel.

Fig. 1 in Paper IV, Henriksen et al. (in prep.) showing a conceptual illustration of fisheries catches (catch per unit effort, (CPUE)) are assumed related to the seasonal abundances of sandeel and the relationship with sandeel emergence might be calculated.
4.3 Describing abundances

The environment is expected to vary with spatial and temporal heterogeneity, which drives the annual magnitude of sandeel abundances in the North Sea. One of the most commonly used estimates of fish abundances in ecology and fisheries science originates from stock assessment model outputs that provide information used in the regulation of fish stocks (Pedersen et al., 1999; Arnott et al., 2002; Maunder and Punt, 2013). These datasets typically provide estimates of recruitment and spawning stock biomass. Hence, recruitment estimates represent early life stages, and spawning stock biomass (or abundances per age-class) represents adults. Recruitment is typically based on information from targeted survey sampling (e.g. egg, larva or juvenile) and adult abundances on fishery catches and surveys. So far, most studies of linkages between the environment and sandeel productivity have used recruitment and adult abundances from stock assessment models to investigate long-term population dynamics in sandeel (Arnott and Ruxton, 2002; van Deurs et al., 2009; Lindegren et al., 2018). This is for good reasons, as the data represents one of the few examples of longer time-series of sandeel population dynamics, because established long-term monitoring surveys (e.g. the International Bottom Trawl Survey (Heessen, 1996)) do not have adequate sampling schemes designed for sampling sandeel.

Currently, sandeel management in the North Sea is divided into seven areas (ICES, 2018), analytical assessments being done for four management areas (Fig. 3, SA1, SA2, SA3 and SA4, ICES (2016)). The temporal trends are presented in brief (Fig. 3). Sandeel recruitment displays a fluctuating trend characterized by negative autocorrelation, where years of low recruitment are followed by a year of high recruitment, although some years can produce extreme recruitment events of several orders of magnitude (e.g. 1996, Paper I). During the last two decades, recruitment has decreased as fluctuations have been less pronounced and the frequency of extreme recruitment events has decreased. Furthermore, a more pronounced negative trend has been observed for the spawning biomass in all areas. Since the early 2000s, the biomass level has been lower than the historic trends, although increasing trends have been observed for northern areas (i.e. SA3 and SA4).
These datasets do have some drawbacks, however, as they basically integrate across large areas with limited seasonal resolution (often just annual or biannual estimates). Thus, the connection and relationship with important life history events can be difficult to detect. Furthermore, as an inherent part of a stock assessment model, adult estimates are always biased by fishing efforts (Murphy, 1965; Gavaris, 1980; Ludwig and Walters, 1985). These shortcomings can be addressed by using sandeel data that is independent of the fisheries (Box 3). Such data can either be used as a supplement (Paper I) to analyse stock assessment model
outputs or stand alone. The latter can be obtained from scientific surveys (Paper II and Paper III) and fisheries (Paper II and Paper IV) (i.e. used as input to the stock assessment model), which represent valuable alternatives to outputs from stock assessment models.

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**Box 3 Data used in papers**

Alternative data sources can be used to complement the analysis of commonly used stock assessment outputs. They can also be important in testing and replicating previous findings. An overview of sandeel data sources for each paper is given below.

1. Data on recruitment was obtained from stock assessment outputs to describe the long-term variability of sandeel abundance, but supplementary data from otolith-based measurement was also used to describe extreme year-classes (Paper I, Henriksen et al. 2018).
2. Data from three sources was used to investigate long-term variability in sandeel densities. The data was derived from a self-sampling programme by the Danish commercial fishing fleet, a scientific survey conducted off Shetland and regional stock assessment output (Paper II, Rindorf et al. 2019).
3. Data from a Danish scientific survey was used to describe long-term abundances of sandeel (Paper III, Henriksen et al., in prep.).
4. Data from Danish commercial fishing fleet catches was used to describe the annual abundance of sandeel (Paper IV, Henriksen et al., in prep.).
5 Drivers of abundances

The role and importance of intrinsic and extrinsic factors have not been fully resolved and are not mutually exclusive. Nevertheless, the impact of life cycle is strong in sandeel, where the division into early life versus adult plays a major intrinsic role that influences how other factors affect sandeel abundances. In addition, intrinsic growth factors (e.g. length, growth rate and condition) can be closely interlinked with extrinsic factors of food availability and/or intrinsic factors of density dependence (Hixon et al., 2002; Zimmermann et al., 2018). Furthermore, the role of spatial variation, temporally delayed (lagged) responses and interaction with indirect factors make it difficult to unravel and pinpoint the driving factors (Ottersen et al., 2010). Despite this, the major driving factors of sandeel population dynamics are reviewed, based on current knowledge and literature, and a series of intrinsic and extrinsic factors that drive sandeel abundances have been described in the following sections.

Research making use of these long-term empirical datasets to test and verify which factors can be considered drivers has received varying attention. A review of these papers (n=17) provided the overview needed of the factors that had been investigated through long-term empirical evidence. Thus, only studies that applied statistical modelling in order to explain long-term variability were included. The majority of studies used population parameters from stock assessment outputs, though for the sake of simplicity, studies using survey indices of age-0 and age-1+ were categorized as recruitment (R) and spawning stock biomass (SSB), respectively. Studies modelling productivity (R/SSB or total stock biomass) were also included. The main findings (Fig. 4) are highlighted in brief below, but please see specific sections for detailed descriptions.
Figure 4. Number of predictors in statistical modelling explaining variability in population parameters (i.e. recruitment (R), spawning stock biomass (SSB) and productivity (R/SSB)). Predictor categories are highlighted in colours and the direction of significant relationships (i.e. negative (Neg) and positive (Pos)) is shown, as well as predictors that showed no relationship (NR).

Measures of food availability (i.e. phytoplankton and zooplankton) show significant positive relationships with all population parameters but can also have a significant negative relationship with recruitment (i.e. interpreted as a top-down control, (Lynam et al., 2013)). Significant density-dependent effects showed both positive and negative relationships for all population parameters. Significant negative relationships with temperature effects were found for spawning stock biomass and productivity. Predation (i.e. only predatory fish) relationships were also found to be negatively correlated with all population parameters. Significant relationships with fishing are only found for the spawning stock biomass. Recruitment and productivity had a significant relationship with broad-scale climate (i.e. teleconnection indices). Recruitment can also have a significant positive relationship with length. After reviewing the factors emphasized in other studies as driving sandeel population dynamics, some key gaps were apparent. Therefore, oceanography and habitat were also included as drivers.
5.1 Intrinsic factors

5.1.1 Density dependence

Density-dependent processes (i.e. positive and negative) are known to influence the abundances of North Sea sandeel (Arnott and Ruxton, 2002; van Deurs et al., 2009; Lindegren et al., 2018). Density dependence is apparent for recruitment, which is reflected in data from assessment model outputs and survey data as a negative autocorrelation (i.e. a year of large recruitment is followed by a year of low recruitment) (Greenstreet et al., 2010; Lynam et al., 2013). Spawning stock densities can also influence recruitment positively, which is a common assumption for studies that have investigated density-dependent recruitment (i.e. inclusion of SSB in models). Even if spawning stock is generally a poor predictor of recruitment (Cury et al., 2014; Szuwalski et al., 2015; Somarakis et al., 2019), then assuming that there is no relationship between spawning stock and recruitment is unrealistic (Hilborn et al., 2017). The boom-and-bust fluctuations in recruitment have been shown to influence available biomass, and positive density dependence can be observed through fishery catches in the years following a large year-class, particularly as age-1 individuals (Pedersen et al., 1999; ICES, 2018).

Arnott & Ruxton (2002) reported evidence of negative density dependence, where productivity (R/SSB, also termed recruitment success) is regulated by the density of previous cohorts of age-1 individuals. This regulation also holds for recruitment and has even been shown to decouple the positive effect of spawning stock biomass in years with large cohorts of these young adults (van Deurs et al., 2009). Research on density dependence in sandeel has focused mainly on similar data output from assessment models. Although differences in the assessment model have changed over time, the data have been driven by the dynamics from the same area (i.e. Dogger Bank, SA1). Hence, doubts may be raised as to the validity of the independence and replicability of previous studies, though Arnott & Ruxton (2002) also included a northern management area (i.e. SA3 in current management) and found consistent results.

The detection of both positive and negative density dependence was briefly revisited by investigating data from a recent model assessment (ICES, 2018) based on current management areas (i.e. SA1, SA2, SA3 and SA4, see ICES (2016b)). Model formulations are the same as those used in previous work (i.e. age-1 individuals referred to as N1 in Arnott & Ruxton (2002), van Deurs et al. (2009), Lindegren et al. (2018)).

These explorations revealed that recruitment in only one of the three management areas was affected by the densities of cohorts of age-1 individuals (Table 2). These findings of negative density dependence in SA1 are consistent with previous investigations in the same
area (Arnott and Ruxton, 2002; van Deurs et al., 2008, 2009; Lindegren et al., 2018). This result is not surprising, as the negative density dependence observed is expected to be closely related to previous studies, being driven by the same dynamics around Dogger Bank. In contrast, negative density dependence was not found in other management areas. Combining all areas in linear mixed models did not change this result. Thus, issues of independence and replicability between studies might be flagged as a causal explanation, since the residual variation in output data from related assessment models is expected to be closely linked.

Research presented in the current thesis (Paper II, Box 4 and Paper III, Box 5) supports these analyses, with no apparent evidence of negative density-dependent effects from older cohorts. These analyses have higher spatial resolution and use alternative datasets that do not have the same shortcomings as stock assessment outputs.

Table 2. Summary statistics for linear models (LM) and linear mixed models (LMM) used for exploratory analysis of density dependence on productivity and recruitment in four management areas (i.e. SA1, SA2, SA3 and SA4). The variables used are productivity (R/SSB), recruitment (R), spawning stock biomass (SSB) and number of age-1 individuals (N1). Slopes estimates (\(\beta\)) and p-values (*p < 0.05, **p < 0.01, ***p < 0.001, Wald Z-statistics) are presented.

<table>
<thead>
<tr>
<th>Model</th>
<th>Formulation</th>
<th>Area</th>
<th>(\beta_1)</th>
<th>(\beta_2)</th>
<th>Years</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>LM</td>
<td>(\ln(R_y/SSB_y) = \beta_1\ln(SSB_y)+\beta_2\ln(N1_y))</td>
<td>SA1</td>
<td>-0.874***</td>
<td>-0.348*</td>
<td>1983-2018</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA2</td>
<td>-0.346</td>
<td>0.012</td>
<td>1983-2018</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA3</td>
<td>-0.907**</td>
<td>-0.034</td>
<td>1986-2018</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA4</td>
<td>-0.757*</td>
<td>0.308</td>
<td>1993-2018</td>
<td>26</td>
</tr>
<tr>
<td>LMM</td>
<td>(\ln(R_y/SSB_y) = \beta_1\ln(SSB_y)+\beta_2\ln(N1_y))</td>
<td>All</td>
<td>-0.562***</td>
<td>0.038</td>
<td>All</td>
<td>131</td>
</tr>
<tr>
<td>LM</td>
<td>(\ln(R_y) = \beta_1\ln(SSB_y)+\beta_2\ln(N1_y))</td>
<td>SA1</td>
<td>0.126</td>
<td>-0.348*</td>
<td>1983-2018</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA2</td>
<td>0.654**</td>
<td>0.012</td>
<td>1983-2018</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA3</td>
<td>0.093</td>
<td>-0.034</td>
<td>1986-2018</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA4</td>
<td>0.243</td>
<td>0.308</td>
<td>1993-2018</td>
<td>26</td>
</tr>
<tr>
<td>LMM</td>
<td>(\ln(R_y) = \beta_1\ln(SSB_y)+\beta_2\ln(N1_y))</td>
<td>All</td>
<td>0.437***</td>
<td>0.038</td>
<td>All</td>
<td>131</td>
</tr>
</tbody>
</table>

Insignificant predictors of spawning stock biomass (SSB) revealed a relatively weak stock-recruitment relationship in three areas (Table 2). Likewise, the lack of effects of spawning stock biomass on recruitment have been found when interactions are neglected in the model (van Deurs et al., 2009). The positive effects of spawning stock biomass on recruitment were only seen in SA2 but became more significant when all areas were combined in a linear mixed model. The latter highlights spawning stock biomass as a potentially important driver overall. However, the result could also be an artefact of the common positive direction of slopes observed for all areas, which can inflate the significance level. Removing SA2 confirmed these
speculations and made the slope insignificant, revealing that models are sensitive to strong correlations. Alternatively, the weak stock-recruitment relationship may be related to the assessment model, where the impact of a fished biomass of spawning stock biomass can hide and suppress any signal on recruitment. However, in combination with research presented in this thesis (Paper III, Box 4), spawning stock biomass is not considered to have a large impact on recruitment, which fits well in the context of short-lived forage fish, for which the stock-recruitment relationship is often weak, and variability in recruitment is imposed mainly by environmental forcing (Vert-Pre et al., 2013; Szuwalski et al., 2015; Pepin, 2016).

Box 4. Short summary of Paper II
Rindorf et al. (2019)

Density dependence was investigated using data with a spatial resolution compatible with the mosaic of habitat patches that sandeel inhabit throughout the North Sea. A combination of data from fisheries (self-sampling and catches), scientific surveys and stock assessment outputs made it possible to test hypotheses of density dependence on different spatial scales (local versus regional). Two different processes of density dependence were detected on local scales. The first process was a shift in space to areas with low mortality when overall recruitment was high, and the second process was an increase in local mortality when local densities increased. When combined, these processes were found to largely compensate for each other. Furthermore, the densities of previous cohorts (age-1 fish) did not affect recruitment.

Fig. 8 in Paper II, Rindorf et al. (2019) showing how the effect of density-dependent mortality (dark grey line) and density-dependent recruitment (light grey line) compensate for each other when combined (black line).
Positive density dependence from the lagged (i.e. $R$ in the assessment model influences SSB after the second year) recruitment on spawning stock biomass was found for SA2, as well as for the overall effect combining all areas (Table 3). Removing SA2 made the overall slope effect insignificant, which might be related to issues similar to those described above (i.e. positive influence of SSB on $R$). However, the most recent investigations presented here (Paper III, Box 5) seem to indicate that the effect of recruitment might be real. This is supported by evidence from a finer scale of the North Sea, where recruitment has great positive impacts on young adults (i.e. age-1, Paper III), which constitute most of the biomass in the majority of years (ICES, 2018).

Table 3. Summary statistics for of linear models (LM) and linear mixed models (LMM) used for explorative analysis of density dependence on spawning stock biomass in four management areas (i.e. SA1, SA2, SA3 and SA4). The variables used are is recruitment ($R$) and spawning stock biomass (SSB). Slopes estimates ($\beta$) and p-values (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, Wald Z-statistics) are presented.

<table>
<thead>
<tr>
<th>Model</th>
<th>Formulation</th>
<th>Area</th>
<th>$\beta_1$</th>
<th>Years</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>LM</td>
<td>$\ln(SSB_y) = \beta_1 \ln(R_{y-2})$</td>
<td>SA1</td>
<td>0.127</td>
<td>1983-2016</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA2</td>
<td>0.310*</td>
<td>1983-2016</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA3</td>
<td>0.190</td>
<td>1986-2016</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA4</td>
<td>0.024</td>
<td>1993-2016</td>
<td>24</td>
</tr>
<tr>
<td>LMM</td>
<td>$\ln(SSB_y) = \beta_1 \ln(R_{y-2})$</td>
<td>All</td>
<td>0.185**</td>
<td>All</td>
<td>123</td>
</tr>
</tbody>
</table>

The shortcomings of previous studies, where findings are based on analogous data of similar origin (i.e. model assessment output and spatial extent), can be addressed by investigating density dependence in data that is independent of assessment models, such as that sourced from fisheries (Paper II) or scientific surveys (Paper III).
Box 5. Highlight from Paper III: Density dependent effects
Henriksen et al. (in prep.)

Density-dependent effects in both positive and negative directions were investigated through mixed models. For early life (i.e. age-0) no intrinsic density dependence was found. Neither positive effects from the adult stock biomass (i.e. age-1 proxy) or negative effects from a previous cohort (i.e. age-1) were apparent. For adults (i.e. age-1) a significant positive effect of lagged recruitment was found to be a driving factor.
5.1.2 Growth
Growth are affected by several extrinsic factors, where prey and temperature plays important roles (Jobling, 1988; Pepin, 1991; Pörtner and Knust, 2007; Houde, 2008). The understanding of the mechanisms assumed to be involved in sandeel growth are well established through both empirical and theoretical work. During the first year of life, growth are expected to follow the “Stage-Duration” hypothesis (Anderson, 1988; Houde, 1989), whereas the growth of adults follow a highly seasonal pattern (Pitcher and MacDonald 1973).

For early life sandeel, the timing of hatching and settlement have been key focal points in relation to how growth affects survival (Gurkan et al., 2013; MacDonald et al., 2018, 2019a). The period from hatching to settlement have been coupled through biophysical and bioenergetic models that explores how critical sizes are important for settlement (Christensen et al., 2008) and overwintering (van Deurs et al., 2011). Initially, the timing of hatching are expected to impact growth through the match with phytoplankton and zooplankton (Eliasen et al., 2011; Régnier et al., 2017; MacDonald et al., 2019b). During the pelagic larval phase, factors such as ocean retention (Paper I), size of zooplankton prey (Simonsen et al., 2006; van Deurs et al., 2015) and temperature (Christensen et al., 2008) are assumed to be important. The timing of metamorphosis are expected to be size-dependent, and the energetic cost and survival during the first overwintering period by post-settled juveniles are expected to be dependent on reaching a critical threshold size (van Deurs 2011). Energy budget model predicts that mortality from starvation due to insufficient growth seem to be the primary factor influencing the abundances of sandeel (MacDonald et al., 2018). However, the empirical evidence for these mechanisms are largely absent in the literature. Currently, only Eliasen et al. (2011) have tried to explain long-term variability in larval abundance with growth and found a positive relationship with mean lengths.

Growth of adults are restricted to a narrow window of feeding (Winslade, 1974b; Pedersen et al., 1999; Bergstad et al., 2002), where sandeel need to build up energy reserves for a non-feeding period of overwintering (Høines and Bergstad, 2001; van Deurs et al., 2011; Wright et al., 2017a) (Paper IV, Box 6). The condition during the feeding period increases drastically in early spring until reaching stable levels around late autumn (van Deurs et al., 2013). Spatial heterogeneity in length and condition are exists within the North Sea, where central and northeastern areas exhibit higher growth (Boulcott et al., 2007; Rindorf et al., 2016).
Empirical studies using growth parameters (e.g. length, growth rate, condition) to explain long-term variability in sandeel abundances are scarce, and the focus in most of these studies seem to be directed towards the availability of food, which ultimately are the main driver of growth. A range of food indices have been used with limited success (Paper I, Lynam et al. 2013, MacDonald, Speirs, et al. 2019) and thus, growth parameters may be an alternative to account for similar variability. In support, the most recent application of length to explain variability in long-term abundances of sandeel in the North Sea are presented (Paper III, Box 7), which provide evidence to classical hypothesis about larval growth, survival and recruitment. Furthermore, the condition (i.e. energy reserves) before the onset of overwintering seem to be a good proxy for how long sandeel can stay submerged in the sand (Paper IV).
Box 7. Highlight from Paper III: Length as an important driver
Henriksen et al. (in prep.)

Length at age was included in statistical models that accounted for spatial and temporal effects of the long-term variability of early life (i.e. age-0) and adult (i.e. age-1) sandeel. It was the main driver for abundance variability of early life sandeel and provide evidence for previous assumptions that have been outlined in theoretical work.

Fig. S1 in Paper III Henriksen et al. (in prep.) showing the average effects of the model, where length is the only driver for early life (age-0) sandeel.
5.2 Extrinsic factors

5.2.1 Habitat

The abundances of sandeel are tightly coupled to the annual timing of hatching and settlement. The specialized life cycle that includes burying behavior of post-settled sandeel requires a close affiliation to specific sandy habitats, where they remain submerged in the substrate for prolonged periods of time. Submergence are evident during night in the feeding season, but can also add up to several months during non-feeding overwintering. Sandeel mainly occur in shallow coastal areas from 15 to 120 m with current flows are high, but prefers depths of 30 to 70 m (Wright et al., 2000; Tien et al., 2017). Preference for particular substrate are evident, consisting of fine gravel and course sand, where larger individuals prefer coarser sediments (Wright et al., 2000; Holland et al., 2005). Specifically, fine silt have an adverse effect on sandeel abundance (Robards et al., 1999; Greenstreet et al., 2010; Tien et al., 2017), where abundance is higher in habitats having low content of silt, 2-10% (Wright et al., 2000; Holland et al., 2005). These sandy habitats have a patchy occurrence throughout the North Sea (Fig. 5). As a consequence of the high site fidelity, movement of older sandeel are limited, and dispersal of sandeel throughout the North Sea are expected to be a product of larval drift, where settlement depends largely on distance to suitable sandy habitat (Gauld, 1990; Christensen et al., 2007, 2008; Jensen et al., 2011; Wright et al., 2019). Several studies applying individual-based modelling schemes have investigated the essential timing of events during hatching to settlement (Berntsen et al., 1994; Proctor et al., 1998; Gallego et al., 2004; Christensen et al., 2008), where the spatial heterogeneity of frontal zone retention favors some areas, such as the Dogger Bank area (Fig. 5, Box 8).
Figure 5. Map showing sandeel fishing grounds, which largely correspond to the distribution of patches of sandy (and gravel-like) habitat in the North Sea (Jensen et al. 2011). Management areas are also shown (i.e. grey patches, SA1, SA2, SA3 and SA4) and examples of inter-bank exchange of sandeel larvae are depicted (i.e. black arrows, showing example of output from a hydrodynamic model from Christensen et al. (2008). The Dogger Bank region is highlighted (dashed line)

How habitat drives long-term population dynamics have not been investigated, but as these habitats are constantly interchanging in morphology (i.e. area, shape and composition) habitat changes could be an important driver for the abundances of sandeel both on local and regional scales (Lanckneus et al., 1994; Dolphin et al., 2007; Lewis et al., 2015). For example, following Maccall's (1990) “basin theory” then density dependent competition for high quality habitat might be driving variability in abundances, where high quality habitat always are occupied by high densities. The most recent research related to this topic, which is presented in this thesis (Paper II), do not assume that habitats change markedly. Nevertheless, sediment composition have been shown to change on a decadal time-scale driven by broad-scale climate fluctuations (See section on Broad-scale climate), resulting in changes in the macrofauna of Dogger Bank, (Wiekung and Kröncke, 2001). Thus, the obvious gap in the understanding on how morphological changes in suitable habitat influences the population dynamics of sandeel, warrant further research.
Box 8. Dogger Bank region in papers

The Dogger Bank is an important region for sandeel in the North Sea. The region probably covers the largest area of interlinked sandy habitat patches and is known to have high retention, which attract recruiting larvae from other habitat patches throughout the North Sea. The highest stock abundances and fisheries catches are observed in the Dogger Bank region. For this reason, some of the most reliable data with longest time-series are available from this region. The region is central in all Papers in this PhD. In Paper II, Paper III and Paper IV investigations have all zoomed in specifically on areas within the region, whereas in Paper I focus is only on this region.

Fig. 1 in Paper I (Henriksen et al. 2018) and Fig. 1 in Paper VI, (Henriksen in prep.) showing areas within the Dogger Bank region that have been investigated.
5.2.2 Food availability
Evidence of diel behaviour (e.g. vertical migrations of larvae and shoaling during feeding by adults) suggests that sandeel are visual feeders that need light to hunt (Winslade, 1974a; Jensen et al., 2003; Freeman et al., 2004). Food availability as a major cause of long-term recruitment variability has been studied on many occasions (van Deurs et al., 2009; Elíasen et al., 2011; Lynam et al., 2013; Eerkes-Medrano et al., 2017) as well as the diet of larvae (Ryland, 1964; Last, 1980; Economou, 1991; de Figueiredo et al., 2007; Malzahn and Boersma, 2009). However, food availability as a driver for adult sandeel has only been sporadically investigated (van Deurs et al., 2014, 2015). Nevertheless, finding the “smoking gun” among a vast range of predictors (i.e. species-specific indices of zooplankton) has proved notoriously hard, with limited success (Paper I, Box 9).

Box 9. Highlight from Paper I: Zooplankton as a driver
Henriksen et al. (2018)

Indices of important species of copepods (i.e. *Calanus* spp.) were investigated during important life history events of hatching. The performance of these indices as drivers of extreme recruitment was tested with limited success. Comparing the performance of different extrinsic drivers showed that only one of four indices tested (i.e. *C. finmarchicus* in February) might be used, but this was outperformed by another driver (i.e. current flow regimes).

Fig. 6 in Paper I Henriksen et al. (2018) showing the time-series of indices of *Calanus* copepods used as a candidate predictor for recruitment.
Examples of significant correlations between sandeel larvae and zooplankton prey have been numerous (e.g. *Calanus* spp., *Arcatia* spp., *Evadne* spp., see Lynam et al. (2013)) but there is great variability on the spatial and temporal scales. In addition, the effect direction can be two-sided, which has been described as processes of bottom-up (positive) regulation by plankton productivity (Frederiksen et al., 2006; Eliasen et al., 2011) and top-down (negative) grazing (Lynam et al., 2013). Nevertheless, a consensus on the importance of *Calanus* copepods seems to be in place, with a mismatch between first-feeding larvae and seasonal appearance of eggs and early stages of *Calanus* copepods having been reported for declines in recruitment (van Deurs et al., 2009, 2014; Régnier et al., 2017, 2019). The relative importance and inclusion of *Calanus* copepods as major drivers of recruitment gets blurred by inconsistent correlations (strong versus weak) between studies, as well as reports of shifts and the flexibility observed in diets (de Figueiredo et al., 2005; Malzahn et al., 2007; Malzahn and Boersma, 2009). This is not surprising when a more detailed overview of the relationship between prey items consumed versus length is explored (Fig. 6), revealing great flexibility in diets. Investigating available research for reported stomach content of larvae showed great flexibility in diet, ranging from non-mobile phytoplankton (e.g. diatoms) over protozoans (e.g. dinoflagellates) to larger traditional mobile zooplankton (e.g. copepods and meroplankton).

Studies on other species of Ammodytidae have shown that detecting and catching prey depend on ontogenetic development, progressive changes in size and swimming ability (Monteleone and Peterson, 1986; Pearre, 1986; McGurk et al., 1992). Simple mean lengths for categories (i.e. dots, Fig. 6) indicated a gradual increase in size with prey switching. This relationship has been investigated in *Ammodytes americanus* (Monteleone and Peterson, 1986), which showed that newly-hatched larvae primarily prey on low-motility prey such as phytoplankton, eggs and protozoans, before switching to nauplii and copepodites. The most obvious switch is to larger prey of adult copepods, which may happen at around 20 mm (Fig. 6). The increased swimming abilities required for hunting seem consistent with the development of dorsal fin rays in *A. americanus* at around 15-20 mm (Monteleone and Peterson, 1986) and observations of gear avoidance at >20 mm for sandeel (Jensen et al., 2003).
Figure 6. Simple overview of stomach data and the reported presence of prey for different lengths of larvae and adult sandeel. The prey was divided into five categories: 1.) non-mobile prey, 2.) small mobile zooplankton, 3.) medium mobile zooplankton, 4.) large mobile zooplankton and 5.) adult prey. Literature references are given (colour). Length range (lines) represents minimum-maximum length of reported presence and mean length (dots) is based on these estimates.

The review also revealed obvious gaps in current knowledge. The majority of studies have investigated early-stage larvae <30 mm, whereas no information exists about the diet of metamorphosed (approx. >40 mm) juveniles. Studies on adult sandeel diet lack detailed descriptions, but calanoid copepods have been reported for all studies, as well as opportunistic feeding and cannibalism on fish larvae (Godiksen et al., 2006; Eigaard et al., 2014; van Deurs et al., 2014). Food consumption seems to be higher when large copepods are available (van Deurs et al., 2014) and mechanistic models have also indicated that a shift from large to smaller copepods roughly halves energy intake, owing to visual constraints and handling time (van Deurs et al., 2015). The long-term effect of food availability has been associated with a shift in the calanoid copepod assemblage in the North Sea from larger *C. finmarchicus* to smaller *C. helgolandicus* (Beaugrand, 2009; Beaugrand and Kirby, 2010; Beaugrand et al., 2014; van
Deurs et al., 2014, 2015). This has also been highlighted as a major driver of declines in forage fish, including sandeel (Clausen et al., 2017; Lynam et al., 2017) and has been shown to coincide with a decrease in length at age in about the late 1980s (van Deurs et al., 2014).
5.2.3 Predation
Engelhard et al. (2014) described sandeel as the most important forage fish in the North Sea highlighting the vital role in the food web as prey for at least 22 species ranging from marine mammals over seabirds to predatory fish. Several studies have highlighted the critical importance of the availability and quality of sandeels for successful reproduction of North Sea seabirds (Rindorf et al., 2000a; Furness, 2002; Frederiksen et al., 2006; Burthe et al., 2012). The sensitivity to low sandeel abundances have also been highlighted for the two pinniped species in the North Sea (Sharples et al., 2009; Sadykova et al., 2017), whereas the importance of sandeel prey to cetaceans varies (Olsen and Holst, 2001; Macleod et al., 2004, 2014; de Boer, 2010). The range of predatory fish that prey on sandeel do not show any direct dependency as seen for other groups. Although, as a group, predatory fish have the greatest impact on the abundances of sandeel, where they are able to exert top-down control (Engelhard et al., 2014). The scientific literature seem to suggest that predation mortality of sandeel vary spatially and the impact should therefore be detected on a small geographical scale. The evidence for so-called “aggregative responses”, defined as many predators aggregating at a site where prey are more concentrated, support such notions (Temming et al., 2004, 2007). High densities of sandeel have been associated with aggregative responses of grey gurnard, lesser weever, whiting and haddock (Pinnegar et al., 2006; Engelhard et al., 2008, 2013).

In general, predation are expected to be one of the main agents for high mortalities in early life stages (Anderson, 1988; Bailey and Houde, 1989). Predation, together with starvation, have been highlighted as the two main drivers for larval assemblages of sandeel (MacDonald et al., 2018, 2019b). Metamorphosis in sandeel are length-dependent and thus, higher growth rates that leads to shorter larval phases should be an advantage (Benoït et al., 2000; Eliasen et al., 2011; Gurkan et al., 2012). After metamorphosis, when juveniles adapt burrowing behavior predation mortality are expected to decrease considerably (Wright et al., 2000). Although, the studies by Cook (2004) indicated that natural mortality of post-settled juveniles (i.e. age-0 sandeel) and young adults (age-1) are equally high (more or less) compared to that of older sandeel (i.e. age 2+). Evidence for the predation from seabirds on juveniles are plentiful (Harris and Wanless, 1991; Wanless et al., 2004) and predatory fish (Temming et al., 2004; Svenning et al., 2005; Weinert et al., 2010), and seem to support higher predation rates in the first year after settlement.

Attempts to explain long-term variability in sandeel populations with predation as explanatory variables are rare and seem to fail (Reilly et al., 2014), because the cumulative impact of several species are hard to estimate and predation from single species seem to be trivial (Engelhard et
Furthermore, correlative studies using outputs from stock assessments are rarely well-matched over the spatial scale due to different area management and thus no analysis was made for this thesis. Yet, ongoing research on how predation (i.e. species, group and ecosystem levels) affects sandeel populations should be encouraged, and food web models (Houle et al., 2013; Heymans et al., 2016) could be suggested as a valuable tool within this context.
5.2.4 Fisheries
Historically, the sandeel fishery in the North Sea dates back to the 1950’s (Macer and Burd, 1970). The fishery increased drastically in the 1970s (Sherman et al., 1981; Nielsen, 1989) and peaked during the late 1980s and during 1990s, where the annual catch exceeded one million tons in some years (Engelhard et al., 2014) (Fig. 7). During the last two decades, it has been the largest single-species fishery in the North Sea, and since the 1990s, the fishery has been dominated by Danish and Norwegian vessels with reported landings of around 64% and 25% of the total catches, respectively (Engelhard et al., 2014). Landings peaked in 1997 and have since decreased together with fleet capacity. Despite the decline in number of vessels, the introduction of newer vessels (i.e. vessel size, engine size, storage capacity, improved trawls) has resulted in a steady increase in fleet capacity (ICES, 2010). Although, the implementation of sound management measures are in place (i.e. follows maximum sustainable yield (MSY) and the precautionary approach in order to ensure a certain threshold biomass that prevent impairment of recruitment) the stock have continued to decrease. The primary reason for the reduction in catches is probably changes in the availability of sandeels to the ecosystem, which have shifted from a high to a low productivity periods caused by a changes in the environment (Clausen et al., 2017). Recruitment have been very low in some areas (i.e. SA2 and SA3), and especially spawning stock biomass have decreased in all areas (Fig. 7).

**Figure 7.** Temporal trends of catches from the fisheries in four management areas in the North Sea (i.e. SA1, SA2, SA3, and SA4).
The availability of sandeel to the fishery in the North Sea is highly seasonal due to the winter burrowing behavior (Macer, 1966; Robards et al., 1999). The highly seasonal sandeel fishery coincides with sandeels feeding period and shoaling behavior (Pitcher and Wyche, 1983; Johnsen and Harbitz, 2013). Thus, the dynamics in the fishable biomass and fishery follows roughly a dome-shaped curve in time (Reeves, 1994), and it is assumed that this reflects the sandeel overwintering and shoaling behavior (Johnsen et al., 2017) and that the initial increase in April and May reflects the gradual emergence from winter dormancy (Paper IV). Currently, the onset of the fishing season is in April (1st in EU-zone and 23 April Norwegian EEZ), around the time when sandeel start emerging daily to feed in large shoals. During the summer, landings decrease as sandeels start to overwinter. Previously catches would increase again at end of the season, as the age-0 fish are exploited, however in the North Sea this age-group is no longer exploited. Hence, the impact of fishing is mainly expected to be directed towards the adult population (ICES, 2018).

There is little doubt that fishing can have immense impact on forage fish (Engelhard et al. 2014), and fisheries impact are assessed every year when the stocks are assesses (ICES, 2018). Yet, a thorough investigation of the long-term impact of fishery pressures (also on a local scale) are missing for sandeel, despite being highlighted as vulnerable to fishing due to regional difference in productivity, reliance of specific sandy habitat and highly stationary behavior. Concerns for local depletion have been suggested for northern banks in SA3 (ICES, 2010; Johannessen and Johnsen, 2015) and SA4 (Rindorf et al., 2000b; Frederiksen et al., 2004), which both have provided basis for the implementation of management that includes closed areas (i.e. rotational and permanent). In this respect, an evaluation fisheries closures, as well as ongoing fishing would provide much needed evidence on the effect of fisheries on sandeel.
5.2.5 Temperature
The central papers dealing with the impact of temperature have reported decreases in sandeel productivity with warming (also termed recruitment success (R/SSB, see Arnott and Ruxton (2002) and Lindegren et al. (2018)). These studies used data from stock assessment outputs for the same large regional area (i.e. SA1). Arnott and Ruxton (2002) included a northern area (i.e. SA3) and found that the effect of temperature were stronger in the southern area. Southern management areas are characterized by shallow waters and therefore the annual temperatures are higher (Rindorf et al., 2016). Data on temperature confirm warmer sea surface temperature (SST) and sea bottom temperature (SBT) in southern areas (i.e. SA1 and SA2), as well as a more narrow range in temperature between bottom and surface compared to northern areas (i.e. SA3 and SA4, Fig. 8). However, the productivity estimates used in these studies do not explicitly resolve whether it is recruitment (i.e. early life) and/or spawning stock biomass (i.e. adults) that are impaired by high temperatures, or both. It is argued that early life, having most of the ontogenetic development in surface waters until settlement, are mainly affected by SST, whereas the biggest impact on adults are via SBT due to their burrowing behavior (Paper III).

![Figure 8](image)

**Figure 8.** Temporal trends of temperature in four management areas in the North Sea (i.e. SA1, SA2, SA3, and SA4). Sea surface temperature (SST) and sea bottom temperature (SBT) are shown.

Studies modelling recruitment as a function of temperature do not point toward any significant relationships with temperature (Eerkes-Medrano et al., 2017), even when accounting for lagged effects (Carroll et al., 2017). The relationship with larval abundances
have even been described as weakly positive (Pitois et al., 2012), but Lynam et al. (2013) highlighted that temperature are more important in structuring the spatial distribution of occurrence than interannual abundances of sandeel larvae. The effect of annual SST was explored using data of recruitment from recent model assessment (ICES, 2018). Significant relationships was only found in SA2 (Table 4). The overall temperature impact combing all areas was also significant, but removing SA2 removed this relationship. The effect observed in SA2 might be real, but based on findings from other studies (Lynam et al., 2013; Eerkes-Medrano et al., 2017)(Lynam et al. 2013, Eerkes-Madran et al. 2017) and research presented here (Paper I and Paper III, Box 10) the consensus points towards temperature as a minor driver for early life. The effects of temperature on early life stages of sandeel seem to play a more indirect role, such as influencing intrinsic factors (e.g. growth and development) that have a direct effect on abundances.

Table 4. Summary statistics of linear models (LM) and linear mixed models (LMM) used for explorative analysis of temperature recruitment in four management areas (i.e. SA1, SA2, SA3 and SA4). The variables used is recruitment (R) and sea surface temperature (SST). Slopes estimates (β) and p-values (*p < 0.05, **p < 0.01, ***p < 0.001, Wald Z-statistics) are presented.

<table>
<thead>
<tr>
<th>Model</th>
<th>Formulation</th>
<th>Area</th>
<th>β</th>
<th>Years</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>LM</td>
<td>ln(R_y) = β_1SST_y</td>
<td>SA1</td>
<td>-0.100</td>
<td>1992-2018</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA2</td>
<td>-0.857*</td>
<td>1992-2018</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA3</td>
<td>-0.662</td>
<td>1992-2018</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA4</td>
<td>-0.681</td>
<td>1993-2018</td>
<td>26</td>
</tr>
<tr>
<td>LMM</td>
<td>ln(R_y) = β_1SST_y</td>
<td>All</td>
<td>-0.515*</td>
<td>All</td>
<td>107</td>
</tr>
</tbody>
</table>

Temperature have the potential to affect these intrinsic factors in early development through several life stages. Recently warming have been shown to inhibit gonad development of adult sandeel (Wright et al., 2017a) and delaying the ovarian development in females (Wright et al., 2017b). The spawned eggs develop faster under higher temperatures provoking earlier hatching of eggs and smaller sizes for hatching larvae (Régnier et al., 2018). These changes in gonad and egg development might contribute to a mismatch in the predator-prey phenology during early life (Régnier et al., 2017). Here, warming are predicted to increase the trophic mismatch between sandeel hatching and important prey (Régnier et al., 2019). Empirical studies on larval growth for sandeel are absent, but temperature are assumed to have a positive relationship with growth and standard metabolic rate (Christensen et al., 2008; van Deurs et al., 2011). These expectations surrounding larval growth originates from a theoretical
framework investigating physical transport, survival and bioenergetics through mechanistic models (Gurkan et al., 2012, 2013; van Deurs et al., 2013). However, these expectations have never been thoroughly tested and existing empirical evidence have failed to find any temperature-mediated larval growth so far (MacDonald et al., 2019b).

Box 11. Short summary of Paper III
Henriksen et al. (in prep.)

Data from scientific surveys offering long-term temporal trends (i.e. 2004-2018) and great spatial resolution (i.e. 9 subareas throughout the North Sea) was used to investigate the effect of different intrinsic and extrinsic factors on early life (i.e. age-0) and adult (i.e. age-1) sandeel. Statistical models that accounted for spatial and temporal effects was applied. Length was the only factor explaining the variability for early life sandeel. Recruitment and temperature had positive and negative effects on adult sandeel. The impacts of temperature varied across the North Sea where it was strongest in southern areas.

Fig. 4 in Paper III Henriksen et al. (in prep.) showing how temperature influences adult sandeel across the North Sea.

Currently, few studies have investigated how temperature might affect the adult segment of sandeel populations. Energy budget modelling suggests that temperature is of minor
importance driving survival of older sandeel (MacDonald et al., 2018). In addition, experimental setups have also failed in detecting any direct lethal effects of older sandeel, but the reproductive investment are reported to be negatively impaired by warming (Wright et al., 2017b, 2017a). The reduction in abundances of sandeel in the northwestern part of the North Sea have coincided with periods of low growth, but temperature did not correlate with growth (MacDonald et al., 2019b). In contrast, Rindorf et al. (2016) showed that growth rate and condition of older sandeel are positively related to temperature. During the feeding season temperature also influences sandeel abundances in the water column and feeding activity positively (Winslade, 1974c; van der Kooij et al., 2008).

Box 10. Short summary of Paper IV
Henriksen et al. (in prep.)

Fisheries data was used to describe the timing of seasonal emergence of sandeel after overwintering. Methods was developed in order to account for the biased data and indicators that inform about the timing of emergence was estimated. Earlier emergence was observed in warm years. A bioenergetic model was used to investigate the physiological mechanisms, which indicates that size and the depletion of energy reserves might play an important role.

Fig. 4 in Paper IV Henriksen et al. (in prep.) showing how temperature and phytoplankton correlates with the emergence (measured as the change in biomass and days between two time steps) of sandeel.
A direct negative relationship with temperature have been shown in statistical models using spawning stock biomass as the response variable (Carroll \textit{et al.}, 2017; Lynam \textit{et al.}, 2017; Free \textit{et al.}, 2019), including lagged effects (Carroll \textit{et al.}, 2017). These findings indicates that the negative relationships found when modelling population productivity (e.g. R/SSB and TSB, see Arnott and Ruxton (2002), Carroll \textit{et al.} (2017) and Lindegren \textit{et al.} (2018)) might be related to the adult fraction of sandeel populations. Exploring this relationship using annual SBT and data of spawning stock biomasses from recent model assessment (ICES, 2019) reported a negative relationship for the two southern areas (SA1 and SA2, Table 5), which is consistent with findings presented in this thesis (\textbf{Paper III, Box 11}). The overall effect of temperature was also significant. Removing SA1 and SA2 did not change the results, which indicates that the effect of temperature as a driving factor is solid, but the mechanistic understanding of how temperature impact adult sandeel have limited evidence. Yet, the latest work indicate that early emergence caused by warming can serve as as can serve as a possible pathway for lower survival after settlement (\textbf{Paper IV, Box 10}).

\textbf{Table 5.} Summary statistics of linear models (LM) and linear mixed models (LMM) used for explorative analysis of temperature spawning stock biomass in four management areas (i.e. SA1, SA2, SA3 and SA4). The variables used is recruitment (R) and sea bottom temperature (SBT). Slopes estimates (\(\beta\)) and p-values (*\(p < 0.05\), **\(p < 0.01\), ***\(p < 0.001\), Wald Z-statistics) are presented.

<table>
<thead>
<tr>
<th>Model</th>
<th>Formulation</th>
<th>Area</th>
<th>(\beta)</th>
<th>Years</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>LM</td>
<td>ln(SSB(<em>y)) = (\beta)SBT(</em>{y-1})</td>
<td>SA1</td>
<td>-0.467**</td>
<td>1991-2017</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA2</td>
<td>-0.614*</td>
<td>1991-2017</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA3</td>
<td>-0.367</td>
<td>1991-2017</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA4</td>
<td>-0.532</td>
<td>1993-2017</td>
<td>25</td>
</tr>
<tr>
<td>LMM</td>
<td>ln(SSB(<em>y)) = (\beta)SBT(</em>{y-1})</td>
<td>All</td>
<td>0.446***</td>
<td>All</td>
<td>106</td>
</tr>
</tbody>
</table>

Based on current knowledge and the most recent investigations (\textbf{Paper III, Box 11}) it is obvious that the impact of temperature are driving the abundances of adult sandeel, whereas temperature are proposed to be a secondary driver for other factors in early life. Furthermore, the effects vary in space, where the strongest effects are observed for shallow southern and southeastern areas in the North Sea. The next steps in evaluating the impact of temperature should focus on the mechanisms involved for adult sandeel, where recent reports on impaired reproductive output (Wright \textit{et al.}, 2017a) and increased vulnerability to predation (\textbf{Paper III}) might be reasonable paths to pursue further.
5.2.6 Oceanography

Several simulation studies have emphasized oceanographic drift as playing important roles for larvae survival and settlement (Berntsen et al., 1994; Proctor et al., 1998; Gallego et al., 2004; Christensen et al., 2007, 2008; Gurkan et al., 2012, 2013). Larvae enter the pelagic environment after hatching and are expected to drift passively with ocean currents until settlement. The drifting phase lasts between 1-3 months before metamorphosis at around 45 mm (Wright and Bailey, 1996). Oceanographic features (e.g. basin circulation, currents, microturbulence, stratification) form the trophodynamic environment that joins larvae and planktonic prey, which determine growth and survival (Werner et al., 1997; Bakun, 1998). These expectations surrounding larval growth and survival in sandeel originate mainly from theoretical work investigating physical transport (Christensen et al., 2007, 2008), survival (Gurkan et al., 2013) and biogenetics (Gurkan et al., 2012) through mechanistic models. Thereby providing a framework for hypothesis testing through empirical data. The importance of oceanographic retention has been emphasized as a driver for variability in recruitment because of increased settlement success (Berntsen et al., 1994). Furthermore, frontal retention has been observed support early life-stages of sandeel in high abundances (Munk et al., 2002, 2009), which may provide high growth and improve survival conditions. The most recent research seem to indicate that specific oceanographic retention features are associated with unusual extreme recruitments at Dogger Bank (Paper I, Box 12). These retention flows seem to match life history events of hatching (Paper I), which might be important for providing the right conditions for survival.

<table>
<thead>
<tr>
<th>Model</th>
<th>Formulation</th>
<th>Area</th>
<th>( \beta )</th>
<th>Years</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>LM</td>
<td>( \ln(R) = \beta_1 PC1 )</td>
<td>SA1</td>
<td>-0.597**</td>
<td>1990-2013</td>
<td>24</td>
</tr>
</tbody>
</table>

A short explorative extension of the most recent investigations (Table 6 and Box 12) showed that the relationship seems to hold for Dogger Bank (i.e. SA1). Thus, specific oceanographic retention regime (i.e. estimates taken from principal component analysis in Paper I) of northerly flowing currents are associated with higher recruitment. These investigations calls for further and more extensive research in understanding how physical oceanography (e.g. basin circulation and frontal features) is structuring the long-term
abundances of sandeel. Efforts should be taken in applying the current mechanistic understanding and existing tools (biophysical models) already available to explore long time-series of empirical data.

**Box 12. Short summary of Paper I**
Henriksen et al. (2018)

Years of unusually strong recruitments was associated with specific current flow regimes moving in a northerly direction in February. February marks the onset of the hatching period of first feeding larvae, which are hypothesized to be a bottleneck for recruitment. The flow regime performed better than other extrinsic factors (i.e. SST, NAO, copepods) as a predictor for high recruitments. Hatch dates calculated from otolith measurements seem to indicate that early hatching larvae from February only survive in years with extreme recruitments, which support a proposed recruitment hypothesis for sandeel.

Fig. 3 in Paper I Henriksen et al. (2018) showing the flow regime through a transect at Dogger Bank (A) and how these are related to each other by clustering into northerly (negative) and southerly (positive) directed flows. Extreme recruitments marked as red dots were only associated with negative flows.
5.2.7 Broad-scale climate

Broad-scale climate variability described by teleconnection indices have been hypothesised to be connected to long-term sandeel productivity and recruitment on several occasions. The associations of these teleconnections to sandeel have been through the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO). The indices describe decadal to multidecadal climate variability (Fig. 9). AMO oscillate between cold (negative) and warm (positive) phases that may last for 20–40 years (Alexander et al., 2014), and the temperature changes are coupled to the ocean-climate system, where water masses with different physical, chemical and biological properties are interlinked by advection and circulation currents (Hátún et al., 2009; Alheit et al., 2014). Thus, AMO have strong association to atmospheric climate variability in the North Atlantic, where NAO is the dominant index driving oceanic conditions (Visbeck et al., 2001). In the North Sea, positive phases favour stronger westerly winds, which is associated with stronger currents and storms in winter.

![Figure 9. Temporal trends of (A) North Atlantic Oscillation (NAO) and (B) Atlantic Multidecadal Oscillation (AMO).](image)

The majority of studies have focused on the NAO, but the reported relationships are inconsistent (Arnott and Ruxton, 2002; van Deurs et al., 2009; Lynam et al., 2013; Lindegren et al., 2018). Contrasting findings include a negative relationship between NAO and productivity in a southern area (Arnott and Ruxton, 2002) and positive correlations with larval
recruitment for two northern areas (Lynam et al., 2013), as well as no correlation with extreme recruitment events in the Dogger area (Paper I, Box 13). The only available study focusing on AMO showed a consistent negative relationship with recruitment estimates from stock assessments in three management areas (i.e. SA1, SA2 and SA3, Lynam et al. (2013)).

**Box 13. Highlight from Paper I: NAO as a predictor for recruitment**

Henriksen et al. (2018)

The performance of the NAO winter index as drivers for extreme recruitment was explored through Risk-Ratio tests and was concluded to be a poor predictor.

Fig. 6 in Paper I Henriksen et al. (2018) showing the time-series of the NAO indices used.

The effects of NAO and AMO on sandeel populations were explored further by investigating the relationship with recruitment and spawning stock biomass (SSB). No significant relationship with NAO was found for R and SSB (Table 7). Significant relationships between recruitment and AMO was evident for all areas except SA1. Combining all areas did not change this relationship. The results are consistent with previous findings reporting that recruitment in SA2 and SA3 is negatively impacted by AMO (Lynam et al., 2013). In opposition to these findings, Lynam et al. (2013) also found a relationship in SA1. However, the models used in Lynam et al. (2013) included additional predictors, which might be a reason for the inconsistency. AMO also had a significant negative effect on SSB in the southern areas (SA1 and SA2) and combining all areas did not change this result. The effect on AMO on adult sandeel (i.e. SSB) has not been investigated before and several explanations for the relationship may exist. For example, Alheit et al., (2019) suggested that regime shifts in the plankton community (Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014) in mid-1990s are most likely caused by the shift observed in AMO. Furthermore, both increases in SST during this period (Alheit et al., 2014), as well as the decreases in concentration and saturation in central North Sea (Quante and Colijn, 2016) may be linked to AMO. These are speculations, but based
on the analysis presented above, AMO was here flagged as a driver for both early life and adults.

**Table 7.** Summary statistics of linear models (LM) and linear mixed models (LMM) used for explorative analysis of broad-scale climate on recruitment and spawning stock biomass in four management areas (i.e. SA1, SA2, SA3 and SA4). The variables used is recruitment (R), North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO). Slopes estimates ($\beta$) and p-values (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, Wald Z-statistics) are presented.

<table>
<thead>
<tr>
<th>Model</th>
<th>Formulation</th>
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<th>$\beta_i$</th>
<th>Years</th>
<th>N</th>
</tr>
</thead>
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<tr>
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<td>$\ln(R_y) = \beta_i NAO_y$</td>
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<td>0.057</td>
<td>1983-2018</td>
<td>36</td>
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<tr>
<td></td>
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<td>SA2</td>
<td>0.033</td>
<td>1983-2018</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA3</td>
<td>0.091</td>
<td>1986-2018</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA4</td>
<td>0.165</td>
<td>1993-2018</td>
<td>26</td>
</tr>
<tr>
<td>LMM</td>
<td>$\ln(R_y/SSB_y) = \beta_i NAO_y$</td>
<td>All</td>
<td>0.084</td>
<td>All</td>
<td>131</td>
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<td>-2.677***</td>
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<td>34</td>
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<tr>
<td></td>
<td></td>
<td>SA2</td>
<td>-0.009</td>
<td>1983-2016</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA3</td>
<td>0.029</td>
<td>1986-2016</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA4</td>
<td>0.021</td>
<td>1993-2016</td>
<td>24</td>
</tr>
<tr>
<td>LMM</td>
<td>$\ln(SSB_y) = \beta_i NAO_y$</td>
<td>All</td>
<td>-0.014</td>
<td>All</td>
<td>123</td>
</tr>
<tr>
<td>LM</td>
<td>$\ln(SSB_y) = \beta_i AMO_y$</td>
<td>SA1</td>
<td>-1.109*</td>
<td>1983-2018</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA2</td>
<td>-2.192**</td>
<td>1983-2018</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA3</td>
<td>-0.460</td>
<td>1986-2018</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SA4</td>
<td>-0.966</td>
<td>1993-2018</td>
<td></td>
</tr>
<tr>
<td>LMM</td>
<td>$\ln(SSB_y) = \beta_i AMO_y$</td>
<td>All</td>
<td>-1.261***</td>
<td>All</td>
<td>131</td>
</tr>
</tbody>
</table>
6. Synthesis and general discussion

Our understanding of the way factors drive fish population dynamics is complex because variations in time and space influence the response signal that is observed. To complicate this issue, a whole range of factors may interact with a driving factor to cause complex effects on fish populations (e.g. (Ottersen et al., 2010; Perry et al., 2010; Planque et al., 2011)). The overarching aim was ultimately to unravel the most important factors driving the abundances of sandeel, but the complexity and overlap of these factors make it difficult. This is intriguing in terms of how complexity might be disentangled, because the factors that contribute to this complexity challenge the science that provides the knowledge and solutions for conserving and managing this important North Sea forage fish. Nevertheless, intrinsic factors such as life cycle and associated life history events are major contributors to the complexity and variability observed in sandeel, but they also serve as focal points for studying the mechanism and dynamics of other factors. This thesis reinforces the early-life and adult developmental phases, which are characterized by distinct life history events, as an essential division for interpreting, reviewing and analysing the driving factors for sandeel. Findings presented in the thesis have provided new insights, as well as supporting and revising previous knowledge about sandeel population dynamics.

The thesis and research provided in papers present a range of statistical tools used to investigate commonly used data (i.e. stock assessment model outputs) as well as datasets from alternative sources (i.e. fisheries and scientific surveys). These sources and methods have made it possible to thoroughly investigate how the population dynamics of sandeel are influenced by a series of intrinsic and extrinsic factors. The findings have reinforced assumptions (Christensen et al., 2008) and the limited empirical evidence (Eliasen et al., 2011) of the importance of intrinsic larval growth for recruitment in sandeel (Paper III). Nonetheless, the availability of food should evidently be argued as the main driver of this relationship, and growth estimates are put forward as an alternative source to describe variation equivalent to a whole catalogue of food predictors previously used (Lynam et al., 2013; MacDonald et al., 2019b). The oceanographic processes that facilitate the trophodynamic arena linking food availability with growth are shown to be a good predictor for unusually large year-classes (Paper I) and are presented as an overarching central driving factor for early-life sandeel, consolidating important life history events of both hatching (Paper I) and settlement. Previous reports on the impact of temperature are thoroughly investigated, and evidence of direct effects is observed for adult sandeel (Paper III). In addition, the effect of temperature is found to vary
spatially and explorative analysis in the thesis supports this pattern. Efforts have been made to understand how temperature affects adult sandeel, and early emergence triggered by warming can serve as a plausible outcome that has several potential implications for survival after settlement (Paper IV). New processes of density dependence on contrasting spatial scales are also introduced (Paper II). Furthermore, previous findings of density-dependent regulation of preceding cohorts are revised (Paper II and Paper III) and are suggested to be an artefact of closely related datasets. Although factors have been outlined separately, they are not mutually exclusive. The interaction between factors in time and space has proved valid through several studies, so a brief presentation is devoted to these mechanisms throughout the life cycle (Fig. 10).
6.1 Factors interact: pathways for driving factors

The pathways (Fig. 10) for influencing early life include several shifts in the ontogenetic development from egg through several larva stages to metamorphosed juvenile. The main life history events include hatching and settlement, which have been highlighted as the bottlenecks for recruitment (Wright and Bailey, 1996; Gurkan et al., 2012). The timing of hatching is important in matching conditions for sufficient growth, where a “critical period” marking the transition between yolk sac and exogenous feeding — so-called first feeding larvae — has have been highlighted as the key determinant for survival (Régnier et al., 2017). Good growth conditions have been linked to the general availability of phytoplankton and zooplankton as food, but close “match-mismatch” (Cushing, 1990) relationships between the production of *Calanus* eggs have also been highlighted (van Deurs et al., 2009; Régnier et al., 2019). Having said that, this important timing of hatching can be set back as a consequence of temperature, directly affecting physiological rates in sandeel, with warming delaying ovarian development (Wright et al., 2017b) and bringing about earlier hatching of eggs due to faster development rates (Régnier et al., 2018). Furthermore, the indirect impact of temperature on food availability has recently been linked to the match with specific *Calanus* copepods (Régnier et al., 2019). Research presented in this thesis introduces oceanographic flow regimes as an important driving factor for these interlinked relationships (Paper I). Since the fate of larvae and their planktonic food sources is largely affected by the same oceanographic processes, it brings together all the chemical, physical and biological properties that provide good conditions for larvae growth and survival (Bakun, 1998). The importance of growth in early life is reinforced by the most recent research presented here (Paper III), with increases in length at age being associated with higher survival to the settlement stage. The timing of settlement is closely related to size-dependent metamorphosis, but settlement success is assumed to be related to the distance to suitable habitat (Christensen et al., 2008; Wright et al., 2019), which is favoured by retention features (Paper I). Factors that favour settlement, such as suitable habitat and retention, occur patchily and thus offer very different probabilities for survival throughout the North Sea (Jensen et al., 2011; van Deurs et al., 2013). Furthermore, reaching a critical threshold size is crucial for the survival of juveniles during the first overwintering (van Deurs et al., 2011; MacDonald et al., 2018). The dynamics of settlement are complicated by density dependent processes that mediate settlement success. The impacts of local density-dependent mortality are detected when sandeel densities are high, but these effects can largely be offset by expanding the spatial occurrence to low-mortality habitats (Paper II).
Figure 10. Illustration showing how intrinsic (inner circle) and extrinsic (outer circle) driving factors (solid arrows) affect early-life and adult sandeel on short-term time scales (annual and biannual). Possible interactions between factors are also shown (dashed arrow). Broad-scale climate is expected to affect ecosystems on long-term time scales (decadal and multidecadal).

After settlement, temperature is a large contributor to the variability observed in the abundances of adults with negative impacts on abundances during overwintering, although the positive density dependence of recruitment success of larvae does impact abundance levels (Paper III). The effect of temperature vary spatially, and consequently susceptibility to temperature is not distributed evenly. The physiological impact of warming is reported to increase the metabolic costs (van Deurs et al., 2011), which leads to reduced reproductive investments (Wright et al., 2017a) and delays in the timing of female oocyte maturation (Boulcott et al., 2017). Furthermore, the depletion of reserves caused by the higher temperature promotes early emergence after overwintering (Paper IV). Depleted energy stores might force foraging behaviour under poor conditions that are outside the main growth period in spring and thus compromise the energy/predation trade-off between energy gain and survival probability (van Deurs et al., 2010). The increase in diel feeding behaviour during prolonged periods increases predation because they are more vulnerable when leaving and entering sediments (Temming et al., 2004; Johnsen et al., 2009). These predation mortalities can have an immense
local impact, when predators aggregate and target high densities of sandeel (Temming et al., 2007; Engelhard et al., 2013). The impact of fisheries is also expected to be higher because more individuals are needed to reach targeted biomasses (i.e. quota). This thesis also provides fresh evidence of broad-scale climate-forcing (i.e. AMO), influencing long-term (multidecadal) abundances of both early-life and adult sandeel—effects that may include dramatic changes in the environment (e.g. temperature and oceanography) that cause a regime shift (e.g. food availability and predation) in ecosystems.
6.2 Perspectives

Sandeel are unlike other North Sea forage fish in that they have specialized life history characteristics that include strategies of burying behaviour. As a consequence, strong site fidelity and low mobility are apparent traits, restricting the distribution of sandeel to specific patchy sandy habitats throughout the North Sea. These life history characteristics increase sandeel’s vulnerability to exploitation and a changing environment. Considering the importance of sandeel as a central part of the North Sea food web, sudden changes can have immense ecosystem-wide consequences affecting plankton assemblages (top-down) and top predators (bottom-up), as well as fisheries opportunities. Solving the recruitment conundrum is central to the variability observed in sandeel, and several outputs from research presented here (Paper I and Paper III) bridge the gaps from previous theoretical work. The merits of that work still need to be investigated further, but the potential for integrating factors into forecasting has already been put forward (Paper I). In this respect, stock assessment models that integrate recruitment forecasting based on physical oceanography have already been developed (Christensen et al., 2009, 2013; Hoff et al., 2013). New insight into density-dependent processes has also been presented, which will enhance our basic understanding of vital demographic processes (Paper II). Moreover, the findings are essential to our understanding of the possible response, resilience and vulnerability to a future with climate change, where projections suggest a warmer North Sea (Quante and Colijn, 2016). This knowledge is important in managing the sandeel stocks that sustain industrial fisheries, while securing prey for sandeel-reliant predators (Hollowed et al., 2013; Dickey-Collas et al., 2014). Reports of stronger effects in the shallow south-central and eastern North Sea (Paper III) serve as a timely warning which may call for precautionary approaches. These areas (i.e. SA1 and SA2) have spawning stock biomasses that have been under the reference points on several occasions within the last decade (ICES, 2018). In addition, the development of research on the influence of temperature (Paper IV) has shown that warming causes early emergence and depletion of energy stores of overwintering sandeel, which might have added implications for management, because as biomass (weight and condition) decreases, catches of (individual fish in numbers) may increase. Furthermore, since sandeel play a major role in the diet of predatory fish, seabirds and mammals (Engelhard et al., 2014), changes in the timing of emergence are likely to affect higher trophic levels. Research initiatives have been presented for most factors (see Sections in thesis).
7. Conclusions

This thesis has sought to combine current knowledge and new findings in relation to the factors that drive the population dynamics of sandeel in order to provide an essential overview that could help our understanding of important mechanisms, as well as encouraging ongoing research initiatives. A framework for reviewing the factors that influence sandeel has been presented in this thesis. Thus, driving factors for sandeel populations have been identified and highlighted for important life cycle periods of early-life and adult sandeel. The assemblage of knowledge gathered provides a much-needed baseline and annotated bibliography for scientists who are interested in sandeel, and insights from explorative analysis will motivate more thorough investigations into topics that have received little attention. Furthermore, a catalogue of analytical tools for investigating the mechanisms involved is presented in papers (see Appendix) and fresh insights into the effect of oceanography, density dependence and temperature are presented. The knowledge obtained is also highly relevant to the future conservation and management of sandeel in the North Sea.
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Oceanographic flow regime and fish recruitment: reversed circulation in the North Sea coincides with unusual strong sandeel recruitment

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*Marine Ecology Progress Series*

607, 187-205, 2018

DOI: https://doi.org/10.3354/meps12945
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Published in:
Marine Ecology - Progress Series

Link to article, DOI:
10.3354/meps12786

Publication date:
2018

Document Version
Publisher's PDF, also known as Version of record

Link back to DTU Orbit

Citation (APA):

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INTRODUCTION


The lack of successful applications of environmental predictors (e.g. physical and biological) to date may be partly due to the strong emphasis placed on the stock–recruitment (S-R) relationship (Ricker 1954), which assumes that recruitment variability (i.e. where
recruitment is understood as the number of young-of-the-year individuals at the life phase transition from larvae to juveniles; ICES 2018) is primarily explained by the biomass of the reproductively active segment of a stock, also termed the spawning stock biomass, and thus any environmental influence must therefore be secondary (Myers 1995, Myers & Barrowman 1996). However, modelled S-R relationships for individual stocks are often weakly supported by the data, due to high inter-annual variability in recruitment, in combination with relatively short time-series (Fogarty et al. 1991, Olsen et al. 2011, Szuwalski et al. 2015). Established correlations are therefore often quite weak, and tend to decompose or change over time (Myers 1998, Skern-Mauritzen et al. 2016).

The perception that recruitment is a function of the biological and physical oceanography dates back a century (Hjort 1914, 1926). Corollaries from this work have since given rise to hypotheses, such as the ‘match–mismatch’ hypothesis (Cushing 1975, 1990), which build on the realization that biological and physical processes might be complementary and emphasize the importance of matches in time and space between the early life stages and the availability of food and the ‘right’ physical conditions. In a recent meta-analysis, Vert-pre et al. (2013) found that although some stocks showed strong S-R relationships, net population increases for the majority of stocks were driven by environmental regimes.

Examples of significant correlations between recruitment and planktonic food resources are common in the literature (e.g. Beaugrand et al. 2003, van Deurs et al. 2009, Burrow et al. 2011, Kristiansen et al. 2011). The fate of fish larvae and food sources are to a large extent influenced by the same oceanographic features, and yet the local oceanographic processes are often neglected in these studies or replaced by higher-level climate indicators such as average temperature or teleconnection indices like the North Atlantic Oscillation (NAO, an index of the predominant air circulation patterns over the North Atlantic) (Arnott & Ruxton 2002, Solow 2002).

The purpose of the present study was to explore the potential for using advanced oceanographic model output in short-term forecasts of fish stock production (i.e. recruitment), which we investigated using a well-studied North Sea case. The ecologically and economically important lesser sandeel Ammodytes marinus stock on the Dogger Bank (DB) in the central North Sea is an example of a fish stock in which recruitment dynamics drive most of the population variability and catch opportunities. This stock is a typical ‘boom-and-bust’ type of stock (Schwartzlose et al. 1999), characterized by dramatic fluctuations and occasional unusually strong year-classes that sustain a large fishery in the following years. Hence, the ability to predict the coming of an exceptionally strong year-class is of major importance (de Moor et al. 2011). The recruitment of sandeel has been linked to both food abundance and climate indicators, such as sea surface temperature (SST) and the NAO (Arnott & Ruxton 2002, van Deurs et al. 2009, Régnier et al. 2017, Lindgren et al. 2018). With respect to food availability, in particular the temporal match–mismatch between occurrence of first-feeding larvae and the abundance of the 2 largest copepod species in the North Sea, Calanus finmarchicus and C. helgolandicus, has been stressed (Arnott & Ruxton 2002, van Deurs et al. 2009, Régnier et al. 2017). Simulation studies of hydrodynamic larval drift and circulation processes that affect larval growth have also been carried out (Christensen et al. 2007, Gurkan et al. 2012), but studies on the connection between local oceanographic events and inter-annual variability in sandeel recruitment do not exist.

The general flow regime of the North Sea can be described as a counterclockwise circulation produced by prevailing southwesterly winds, which occasionally reverses with easterlies. This occasional shift from the predominant counterclockwise circulation to other regimes can include a large-scale gyre flowing in the opposite direction over the whole North Sea or multiple smaller-scale gyres with alternating flow directions and even temporary circulation halts (Kauker & von Storch 2000, Sündermann 2003, Sündermann & Pohlmann 2011). Changes in the physical setting affect fish production, especially for forage fish that display boom-and-bust dynamics (Fréon et al. 2005). For example, upwelling events driving the production of Pacific sardine stocks off the coast of Central America (Rykaczewski & Checkley 2008) are strongly linked to certain types of ocean circulation patterns. Another example is the Norwegian spring spawning herring, where the physical conditions of the Norwegian Coastal Current determine survival and growth of the larvae as they drift toward the nursery grounds in the Barents Sea (Skagseth et al. 2015).

During a preliminary investigation, it was observed that the largest sandeel recruitment event on record coincided with a circulation shift in the northwest Atlantic during the winter of 1996, first mentioned by Greene & Pershing (2003) and later coupled to possible circulation reversals in relation to settlement dynamics of 2 species of flatfish in the North Sea (Lacroix et al. 2013, Tiessen et al. 2014). While many
studies have flagged hydrodynamics as playing various roles for sandeel recruitment involving different biophysical levels and larval life stages (Berntsen et al. 1994, Proctor et al. 1998, Gallego et al. 2004, Christensen et al. 2007, Gurkan et al. 2013), they all agree on the notion that at least the earliest life stages, or first-feeding larvae, should be considered as passive tracers whose fate is dictated by the ocean currents. Although sandeel larvae develop active swimming abilities before they metamorphose at a length of ~40 mm, it is assumed that they generally follow current surface flow until settlement (Christensen et al. 2008). The drifting phase lasts from 1–3 mo (i.e. February to April) (Wright & Bailey 1996, Conway et al. 1997, Jensen et al. 2003).

We therefore hypothesized that unusual strong year-classes of DB sandeel are associated with certain types of flow regimes during the early parts of the drifting period when first-feeding larvae are most abundant. Flow regimes were quantified using original output from an oceanographic model (HIROMB-BOOS), and the period of first feeding was examined from hatch dates estimated using larval otoliths. Subsequently, the oceanographic output was subjected to a cluster analysis to tease apart different types of flow regimes, before relating these to sandeel recruitment. To test the usefulness of flow regimes in short-term forecasting of strong year-classes, we used a probabilistic approach. This approach, also known as the risk-ratio analysis, is widely used in risk assessments (Wilson & Crouch 1987), but rarely applied in fisheries science (but see Mantzouni & MacKenzie 2010 and Skagseth et al. 2015). Nevertheless, it may be suitable for detecting mechanisms associated with infrequent extreme year-classes, as seen for our case stock. We applied this approach to the flow regime data that resulted from the cluster analysis, as well as to other environmental variables previously suggested to be influencing sandeel recruitment. This comparative approach not only allowed us to rank the performance of the different recruitment predictors, but it also provided a basis for discussing possible causal mechanisms.

**MATERIALS AND METHODS**

**Oceanographic data**

We inspected 3 papers (i.e. Kauker & von Storch 2000, Sündermann 2003, Sündermann & Pohlmann 2011) in order to identify an oceanographic time-series of flow regimes that captured the essentials of the Central North Sea water circulation system as well as the transport of water over the DB, where the most important sandeel fishing grounds are located. Based on these studies, we settled on a transect that followed the 50 m depth contour, along the northern edge of the DB, stretching from the centre of the North Sea to 60 nautical miles (n miles) from the UK coastline (0.0° E, 55.5° N to 4.0° E 56.0° N), the latter to avoid the influence of the Scottish coastal current (i.e. Brown et al. 1999) (Fig. 1). Based on the assumption that first-feeding larvae are passive drifters distributed in the water column (e.g. Christensen et al. 2007), hourly values of the net flow of surface water (0–15 m depth) were then derived by summing up 3D water fluxes from an oceanographic model (described in more detail below).

Otolith-based estimates of hatch dates in the Shetland sandeel population, early-stage larvae captured over the DB by the Continuous Plankton Recorder (CPR), and peak larval survival estimated by individual-based modelling (Wright & Bailey 1996, Gurkan et al. 2013, Lynam et al. 2013) seem to indicate that February and March covers the most important period for first-feeding larvae; thus we chose to focus on these months in the data analysis (this assumption was tested later in the present study; see ‘Estimation of hatch dates’, below).

The oceanographic data were provided by the Danish Meteorological Institute (DMI) and are a validated hindcast (1990–2013) produced by the North Sea-Baltic Ocean Model (HBM Model) in the operational setup used by DMI (http://ocean.dmi.dk/models/hbm.uk.php). The model is a 3D ocean circulation model, where the vertical flow assumes hydrostatic balance and incompressibility of sea water, and horizontal transport is modelled using the Boussinesq approximations (Smagorinsky 1963, Canuto et al. 2002, Berg & Poulsen 2012). The horizontal resolution (grid spacing) was 6 n miles, which is a standard resolution used by DMI for coarse-scale applications, and has previously been used to model fish larval drift in the North Sea and water fluxes between the North Sea and the Baltic Sea (e.g. She et al. 2007, Gurkan et al. 2013, Ulrich et al. 2017). The main consequence of this relatively coarse grid spacing is the potential risk of failing to capture the full effect of small-scale eddies and the risk of exaggerating the wind effect. However, in the present study, we were only interested in the trends in net flow averaged across 300 km wide transects (i.e. the geographical scale of interest is 27 times larger than the model resolution), where small-scale processes are likely to be averaged out as fluctuations along the transect. The model was forced by atmospheric data from a numer-
ical weather prediction model, High Resolution Local Area Model (HIRLAM, http://hirlam.org/), with 10 m wind fields, sea level pressure, temperature, humidity, and cloud cover. At open model boundaries between Scotland and Norway, and in the English Channel, we used tide surges from a barotropic model of the North Atlantic (Dick et al. 2001). All other model variables at open boundaries were set to monthly climatological values. The freshwater daily river runoff data come from the operational hydrological model HBV run by the Swedish Meteorological Hydrological Institute (Bergström 1992) and observations made by German Bundesamt für Seeschifffahrt und Hydrographie. The hindcast period (1990–2013) was limited by the overlap of applied forcing data sets.

In the present study, we expressed the net flow of water across the transect as the signed (i.e. ±) accumulated length (km) of water that has moved through the transect since time 0, averaged across the surface of the transect (where ‘+’ indicates water movement from north to south and ‘−’ indicates the opposite movement, from south to north). Time 0 was either 1 February or 1 March, and the final dataset consisted of hourly values for all of February and March, respectively. To get from length of water to the volume of water, we must multiply by the dimensions of the transect surface area, which was 300 km (transect length) times 0.015 km (transect depth), and the hourly average transport rate can be derived from the volume at time \( h \) minus the volume at time \( h - 1 \). However, in relation to the present study, the length of water was found to be the most useful unit, as it offers a direct approximation of the scale of potential horizontal transportation of passively drifting biological particles (such as fish larvae or copepods).
Identification of flow regimes using principal component analysis and hierarchical clustering

To identify distinct annual and monthly flow regimes, we carried out a principal component analysis (PCA) on hourly values of the accumulating water transport across the selected transect. PCA is a useful statistical signal-processing technique to reduce the multi-dimensionality of datasets for pattern recognition. The PCA algorithm constructs principal components (PCs) obtained as linear combinations of the original variables, where the first PC is allowed to have the largest possible variation in the data, and the second PC is estimated under the assumption of being orthogonal to the first PC and to have the largest possible variance, and so forth for other additional PCs that might be important (see Abdi & Williams 2010 for details). In order to choose the correct number of PCs to be kept in the analysis, we used a scree test (Cattell 1966), which is a graphical detection of a bend in the distribution of the successive variance explained.

Data from February and March were treated in 2 separate PCAs, which assigned each year in the study period to clusters, each of which represented distinct hydrodynamic patterns (hereafter referred to as flow regimes). The Euclidean distances between years were computed from the projection of years on the PCs, and subsequently a hierarchical clustering analysis was conducted. We used the Ward linkage method (Ward 1963), which has a minimum variance criterion that minimizes the total within-cluster variance. For each step, we identified a pair of clusters which leads to a minimum increase in total within-cluster variance when merged. The PCA and the hierarchical clustering analysis were implemented in the R-packages ‘PTA-k’ (Leibovici 2010) and ‘ade4’ (Chessel et al. 2004).

Sandeel recruitment

As a measure of sandeel recruitment on the DB, we used the number of young sandeel in July (age 0) as estimated by the International Council for the Exploration of the Sea (ICES) for Management Area 1 (ICES 2016a). These recruitment estimates are produced by a stochastic multispecies stock assessment model (Lewy & Vinther 2004) and are essentially back-calculated in the model from the number of 1 yr old sandeel estimated by the model in the following year using the natural mortality for age 0 sandeel in the second half year (ICES 2016a). Prior to the update of recruitment time-series in March 2017, input to the stock assessment model used by ICES was changed. We therefore included recruitment time-series from before and after the 2017 update (ICES 2016b, 2018).

Estimation of hatch dates

To identify and confirm the important months (i.e. February/March; Gurkan et al. 2013, Lynam et al. 2013) of first-feeding larvae in the DB area, we derived hatch dates from sandeel otoliths taken from larvae caught on the DB in 2006, 2008, and 2009. All larvae samples were collected between 17 and 22 April. The larvae were caught with a 1 m Methot-Isaac-Kidd (MIK) net, then frozen at sea and later thawed and preserved in ethanol. Three MIK samples were randomly selected from each year (9 samples in total). From each sample, 20 larvae were subsampled using a stratified sampling procedure to cover the full length distribution. Otoliths were dissected from the larvae under polarized light, imbedded in thermoplastic cement, and then photographed under a microscope. Daily increment widths were measured from the central primordium to the otolith edge, but not all increments were visible. Hence, the age in days was determined by dividing the distance from yolk sac absorption to the otolith edge by the mean daily increment width and then adding 12 d to account for the yolk sac period (Wright 1993, Wright & Bailey 1996). The distance along the axis of fastest growth from the primary primordium to the point of yolk sac absorption was assumed to be 20 µm (Wright 1993). A linear age−length relation derived from the subsampled otoliths was then used to convert the length distribution in the original MIK sample to a hatch date distribution. Lastly, each hatch date distribution was corrected for natural mortality. Daily mortality rates ranging between 0.042 and 0.07 (Fujiwara et al. 1990, Régnier et al. 2017) have previously been assumed, and we therefore investigated the sensitivity of mortality. In order to make our results directly comparable to those of Wright & Bailey (1996), we adopted a mortality rate of 0.07, but we also included high (0.12) and low (0.01) mortality rates by simply increasing mortality by ~100%.

Quantifying and comparing the performance of different predictors of recruitment

Previous studies have reported positive relationships between sandeel recruitment and Calanus...
copepods and negative relationships with SST and
the present study, we wanted to re-investigate all
of these recruitment predictors together with our
new oceanographic predictor. Information about the
abundance of *C. finmarchicus* and *C. helgolandicus*
were acquired from the CPR programme. These data
were provided by the Sir Alister Hardy Foundation
for Ocean Science (SAHFOS), and came as monthly
indices calculated specifically for Management Area
1 that covers the DB (ICES 2016b). The NAO was
downloaded as station-based monthly values from
the Hurrel data base: https://climatedataguide.ucar.
edu/climate-data/hurrell-north-atlantic-oscillation-
nao-index-station-based. SST was downloaded from
the Hadley Centre observational database as month-
ly values in a 1 × 1° grid. For the present study, we
used the average SST for an area defined as 1−3° E
and 54−55° N. Only data from February and March
were included in the analysis to match the period of
first feeding and the oceanographic data (see explana-
tion above). One exception to this rule was NAO,
where we used an early (mean NAO for the period
from December to February) and a late winter index
(mean NAO for the period from January to March)
instead of monthly values.

In order to compare the different candidate recruit-
ment predictors, we computed the risk-ratio (RR) as
in Mantzouni & MacKenzie (2010):

$$RR = \frac{G}{(g+G)} \frac{C}{(c+C)}$$  (1)

where *G* is the number of years where favourable
environmental conditions coincided with good re-
cruitment (i.e. unusually strong year-classes), *g* is the
number of years where favourable conditions did not
coincide with good recruitment, *C* is the number of
years where unfavourable conditions coincided with
good recruitment, and *c* is the number of years where
unfavourable conditions did not coincide with good
recruitment. In cases where *G* or *C* was 0, we re-
placed 0 with 1/24, since we have 24 observations in
total.

Since the intention was to forecast the most ex-
treme recruitment events rather than the stock
trends, good recruitment was defined as recruit-
ments that exceeded the mean of the time-series plus
1 SD. This approach suited its purpose and captured
the distinct spikes in the recruitment time series,
which are of particular importance in relation to
managing boom and bust stocks (de Moor et al.
2011). Based on the previously mentioned reports of
a positive relationship between sandeel recruitment
and *Calanus* copepods and negative relationships for
SST and NAO, we defined favourable conditions in
relation to each of those predictors as values either
above or below the time-series mean ± 1 SD. RR > 1
indicates that the probability of observing good
recruitment when the environmental condition is
expected to be favourable is higher than the proba-
bility of observing good recruitment when the envi-
ronmental condition is unfavourable. Hence, high
values of RR were considered indicative of high per-
formance in relation to recruitment forecasting. We
also applied the same RR approach to derive RR val-
ues for the opposite question, i.e. the relative proba-
bility of seeing less than good recruitment when
environmental conditions are favourable (i.e. RR =
\(\frac{g}{G} + \frac{c}{c+G}\)). In this test, low RR values were
considered indicative of high performance. To distin-
guish between the 2 different applications of the RR
equations, we used RR1 and RR2 to label the former
and latter application, respectively. Finally, we
obtained p-values by applying the chi-squared test of
independence to a 2 × 2 contingency table:

$$\begin{bmatrix}
G & g \\
C & c
\end{bmatrix}$$

The p-values refer to the null hypothesis that the 2
categorical variables (environmental condition and
recruitment) are independent.

RESULTS

The net flow of water across the selected transect
(analysed for February and March) went from being
almost consistently positive (i.e. running in a north−
south direction) or negative (i.e. running in a south−
north direction), through highly variable, alternating
between positive and negative, to nearly stagnant
(Fig. 2A,C). The classification of clusters was mainly
driven by the overall direction of the net flow (posi-
tive or negative), but the temporal development of
the trajectories was also important. Division of years
into clusters was based on 2 PCs (PC1 and PC2,
Fig. A1 in the Appendix), together explaining 93.0
and 94.5% of the total variation in February and
March, respectively (Fig. 2B,D). These clusters cap-
tured certain types of flows: (1) unidirectional flow
and relatively large negatively or positively signed
net flow (advection), (2) bidirectional flows associ-
ated with negatively or positively signed low net flow
(retention), (3) relatively weak or stagnant flow that
suddenly shifts to a negatively or positively signed
directional flow of higher net flow (shifting flow), and
(4) relatively weak flow alternating between positive and negative flow centered around 0 (stagnant).

PC1 explained most of the variation (76.9 and 84.8% for February and March, respectively) and discriminated among the types of flows listed above, making a distinction between years of predominantly positive net flow and years of predominantly negative net flow, which represented 2 overarching clusters in both February and March (Fig. 3) and are hereafter referred to as negative and positive flow regimes. However, each flow trajectory was also associated with a temporal behaviour over the transect, for example whether a flow trajectory had a flow with a directional motion, either a continuous or oscillating motion over the transect, or a motion with close to 0 flow in any direction. This temporal behaviour was captured by the second PC2, explaining 16.1 and 9.7% of the variation in February and March, respectively (Fig. 2). The years also had correlations with and total contributions to each PC that supported this (Figs. A2 & A3). The PCA identified 5 different types of flows in February, but only 4 in March, where the analysis failed to distinguish between advection and retention (Figs. 2 & 3).

The year 1994 differed from all other years (in February), as it went from almost stagnant to the highest continuous negative flow observed; thus it is essentially an intermediate between the ‘stagnant’ and ‘retention/advection’ flow types, which is also why the analysis places this year in its own sub-cluster labelled ‘shifting flow’ (Figs. 2 & 3, green). Another outlier was 1991 (March), characterized by an ex-
tremely stagnant flow and net transport close to 0 (Figs. 2 & 3, purple). Also noteworthy was the decreasing trend in net flow in February, where all years (except 2000) assigned to the cluster of positive ‘retention’ flows appeared after 2002. Likewise, only 1 year after 2002 was assigned to the cluster of positive ‘advection’ flows (2012, the weakest among the advection years). Hence, it appears that a shift in the winter oceanography in February from an advection-dominated system to a retention-dominated system occurred around 2002 (Fig. 3A).

Good recruitment (i.e. recruitment > mean + 1 SD) was observed in 1994, 1996, 2001, and 2009 (Fig. 4). In February, all 4 years with good recruitment were assigned to the same overarching cluster consisting of negative flow regimes. However, only 1996 and 2001 were assigned to negative flow regimes in both February and March (Fig. 3). Furthermore, 3 out of the 4 good recruitment years were assigned to the same sub-cluster of negative ‘retention’ flows. Only 1994 was assigned differently and placed (as the only year in the February time-series) to a sub-cluster labelled ‘shifting flow’ (the flow phenomenon of 1994 is described in more detail above, this subsection).

According to the analysis of daily increments in larval otoliths, hatching was mainly confined to March. The earliest hatching occurred on Day 53 (22 February) and the last hatching on Day 83 (24 March). Mean time of hatching also varied between years (by ca. 10 d). Hatching in February was only observed in 2009, whereas in 2006 and 2008 all hatching took

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**Fig. 3.** (A,C) Hourly values of accumulated net transport depicted by year (each small black dot represents a single hourly transport value) and (B,D) dendrograms of the hierarchical clustering, for February (A,B) and March (C,D). Colouration appears in the time-line graphs in panels A and C at high densities of hourly transport values (at very high densities, the coloured area spreads out horizontally; note also that colours are comparable to the dendrograms in B and D and to the colour schemes used in Fig. 2A). The dendrograms split years into 2 overarching clusters: one with predominantly positive and one with predominantly negative flow regimes. The overarching clusters are split further into other sub-clusters. Red bullet points highlight years with distinct recruitment spikes (see Fig. 4 for good recruitment years).
place in March (Fig. 5). The sensitivity analyses showed that mortality did not have a substantial effect on the hatching distributions. A given percentage hatching was reached earlier with increased mortality, but the maximum difference between the low and high mortality scenarios was 5 d (Fig. 5).

In the first RR test (RR1), the flow regime in February performed better than all other recruitment predictors. In fact, the RR1 values computed for the flow regime in February suggested that the probability of observing the combination of good recruitment and a negative flow regime was 243 times higher than the probability of observing the combination of good recruitment and a positive flow regime. In support of this result, the chi-squared test revealed a significant relationship between the distribution of recruitment and the distribution of flow regime in February (i.e. rejecting the null hypothesis of independence: \( \chi^2 = 7.91, p = 0.005 \); Table 1). In comparison, the corresponding RR1 for the negative flow regimes in March and *Calanus finmarchicus* in February was only 5.00

Table 1. Risk ratios (RR) and chi-squared test of independence for various sandeel recruitment predictors. \( G, g, C, \) and \( c \) correspond to the values entered into the RR formulas (RR1 and RR2) (see ‘Materials and methods; Quantifying and comparing …’ for more details). Note that high performance of a predictor is indicated by large RR1 values and small RR2 values. Chi-squared statistics and p-values refer to the null-hypothesis that the 2 categorical variables (environmental condition and recruitment) are independent. The tests were performed on 2 × 2 contingency tables

<table>
<thead>
<tr>
<th>Environmental predictor</th>
<th>( G )</th>
<th>( g )</th>
<th>( C )</th>
<th>( c )</th>
<th>RR1</th>
<th>RR2</th>
<th>Chi-squared</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Negative flow regime (February)</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td>17</td>
<td>243.43</td>
<td>0.43</td>
<td>7.91</td>
<td>0.005</td>
</tr>
<tr>
<td>Negative flow regime (March)</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>18</td>
<td>5.00</td>
<td>0.55</td>
<td>1.50</td>
<td>0.221</td>
</tr>
<tr>
<td>High <em>Calanus helgolandicus</em> abundance (February)</td>
<td>0</td>
<td>2</td>
<td>4</td>
<td>18</td>
<td>0.11</td>
<td>1.20</td>
<td>0.00</td>
<td>1.000</td>
</tr>
<tr>
<td>High <em>C. helgolandicus</em> abundance (March)</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>18</td>
<td>2.33</td>
<td>0.78</td>
<td>0.00</td>
<td>1.000</td>
</tr>
<tr>
<td>High <em>C. finmarchicus</em> abundance (February)</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>20</td>
<td>10.78</td>
<td>0.02</td>
<td>5.35</td>
<td>0.021</td>
</tr>
<tr>
<td>High <em>C. finmarchicus</em> abundance (March)</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>19</td>
<td>3.67</td>
<td>0.58</td>
<td>0.11</td>
<td>0.741</td>
</tr>
<tr>
<td>Low NAO (February)</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>18</td>
<td>2.33</td>
<td>0.78</td>
<td>0.00</td>
<td>1.000</td>
</tr>
<tr>
<td>Low NAO (March)</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>17</td>
<td>0.67</td>
<td>0.67</td>
<td>0.81</td>
<td>0.369</td>
</tr>
<tr>
<td>Low SST (February)</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>18</td>
<td>2.33</td>
<td>0.78</td>
<td>0.00</td>
<td>1.000</td>
</tr>
<tr>
<td>Low SST (March)</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>18</td>
<td>2.33</td>
<td>0.78</td>
<td>0.00</td>
<td>1.000</td>
</tr>
</tbody>
</table>

Fig. 4. Sandeel recruitment. Two recruitment time-series are presented: ICES (2016a) (solid line) and ICES (2016b) (black dashed line) (see ‘Materials and methods’ for details). Good recruitment years (unusual recruitment spikes extending beyond the dashed line) are highlighted with red bullet points (ICES 2016a) or green bullet points (ICES 2016b). Red and green dashed lines: corresponding mean (±1 SD)

Fig. 5. Cumulative hatch-day frequency. Hatch dates were estimated from larval length distribution and the age–length relationship found by otolith daily increment analysis for sampled years: 2006 (red), 2008 (green), and 2009 (blue). Hatch frequencies were corrected for cumulative mortality assuming different mortality rates of 0.01 (circles), 0.07 (triangles) and 0.14 d\(^{-1}\) (squares). DOY: day of the year

regime in February suggested that the probability of observing the combination of good recruitment and a negative flow regime was 243 times higher than the probability of observing the combination of good recruitment and a positive flow regime. In support of this result, the chi-squared test revealed a significant relationship between the distribution of recruitment and the distribution of flow regime in February (i.e. rejecting the null hypothesis of independence: \( \chi^2 = 7.91, p = 0.005 \); Table 1). In comparison, the corresponding RR1 for the negative flow regimes in March and *Calanus finmarchicus* in February was only 5.00
and 10.78, respectively (ranking third and second best), and the distributions of recruitment and flow regime were independent (i.e. the null-hypothesis of independence could not be rejected). In the second RR test (RR$^2$), *C. finmarchicus* in February performed best ($RR^2 = 0.02$, $\chi^2 = 5.35$, $p = 0.021$; Table 1). For example, the relative probability of observing less than good recruitment in combination with a high abundance of *C. finmarchicus* was very low. However, it should be noted that only 2 years qualified as high *C. finmarchicus* abundance years (1994 and 2009). Time-series of *C. helgolandicus*, *C. finmarchicus*, NAO, and SST are presented in Fig. 6.

**DISCUSSION**

**Circulation patterns in the North Sea**

The common circulation in the North Sea is counterclockwise, produced by prevailing south-westerly winds (Sündermann 2003, Sündermann & Pohlmann 2011), but occasionally the flow direction is reversed (i.e. clockwise circulation). According to reports by Greene & Pershing (2003) and Tiessen et al. (2014), such an event took place in 1996. In the present study, the year 1996 was assigned to the overarching cluster encapsulating negative flow regimes in both February

![Time-series of the candidate recruitment predictors for February (left column) and March (right column). Note that in case of the North Atlantic Oscillation (NAO), we applied an early (December to February) and a late (January to March) winter index, as opposed to selecting single months. The red bullet points highlight the years expected to result in highly favourable conditions for sandeel larvae survival (i.e. extending beyond the time-series mean ± 1 SD, as indicated by a horizontal dashed line). Note that while high values of *Calanus finmarchicus* and *C. helgolandicus* are expected to represent favourable conditions, the opposite is true for NAO and sea surface temperature (SST; see 'Materials and methods' for details)
and March and the ‘retention’ sub-cluster in February (in March the PCA could not distinguish between ‘advection’ and ‘retention’ flow types). Considering February in isolation, 7 out of the 24 years analysed were allocated to the cluster of negative flow regimes. However, 2 of these years were classified as ‘stagnant’ or ‘shifting flow’ and not ‘retention’ (in the sub-clusters) and thus whether all 7 years correspond to a reversed (clockwise) circulation on a regional scale (as in 1996) is not clear from the present results.

The schematic illustration by Sündermann & Pohlmann (2011) of the overall circulation in the North Sea suggested 5 possible patterns, of which Kauker & von Storch (2000) provided the most detailed description presented by a 15 yr simulation (1979–1993) using the European Centre of Medium-Range Weather Forecast reanalysis and an ocean circulation model. Here the dominant regime displayed a circulation pattern of large gyres circulating either in a counterclockwise or clockwise direction resulting from northeasterly and southwesterly winds, respectively. In line with our findings, clockwise rotations, represented by negative associated flow regimes in our data, are relatively unusual, taking place only 15% of the time (and in 22% of the trajectories analysed in our study). In comparison, clockwise directions occur 30% of the time. The ‘stagnant flow’ observed in our study was also identified by Kauker & von Storch (2000) and, as in our study, these were also relatively rare (10% in their study and 6% in our study). Kauker & von Storch (2000) also pointed out that it was rare for regimes to last for longer periods, and only 20% persisted for >5 d. Some of the flows that they characterized as stagnant may therefore be comparable to what we refer to as ‘shifting flow’ (which we observed in 6% of the trajectories analysed). They also described a fourth intermediate type of circulation, which occurred 45% of the time, and the full nature of which we may not have captured within our study design. In this type, northwesterly or southerly winds produced bipolar circulation structures, shifting between southern and northern parts of the North Sea, which might be translated to either ‘shifting flow’ or ‘retention’ in our case.

Another remarkable pattern emerging from the present analysis was that during the first half of the time-series (1990 to ca. 2002), flow regimes of the ‘advection’ type dominated in February, whereas in the latter half of the time-series, flow regimes of the ‘retention’ type prevailed. Such an indication of an oceanographic regime shift is striking, in particular because a series of other studies have documented recent biological regime shifts in the North Sea, such as shifts in the zooplankton species composition and reduced growth and recruitment of planktivorous fish, including sandeel (e.g. Reid et al. 2001, Beaugrand 2004, Clausen et al. 2018, Lindgren et al. 2018). However, these shifts typically occurred around 1990 (plus/minus several years), which represents the beginning of the time-series analysed in the present study, and therefore prevented us from aligning the findings from previous regime-shift studies with our data.

**Flow regimes in relation to sandeel recruitment and first feeding**

All 4 good recruitment years (i.e. unusually strong year-classes, see definition of ‘good’ in ‘Materials and methods’) coincided with negative flow regimes in February (only 2 in March), suggesting that the flow regimes in February, rather than in March, determine the fate of sandeel larvae on the DB. In the present study, otolith-based hatch dates were mainly confined to March, which corroborates similar studies from nearby sandeel populations (Shetland Islands and Firth of Forth), showing peak hatching in the same month (Wright & Bailey 1996, Régnier et al. 2017). In contrast, the CPR survey also captured substantial numbers of sandeel larvae on the DB in February (Lynam et al. 2013), indicating that the otolith-based approach may be biased toward relatively late hatch dates. With this in mind, a closer inspection of the hatch date distributions revealed a heavy tail into February in 2009, which happened to coincide with a negative flow regime and the second largest recruitment event in the time-series. In fact, Wright & Bailey (1996) also observed a similar extended tail in the 1990 hatch data distributions, which coincided with a large year class (Poloczanska et al. 2004). Hence, we suggest that negative flow regimes in February facilitate better first-feeding conditions and survival of the earliest larvae, creating the extended tails that we observed in the otolith-based hatch date distributions. This view is in line with Arnott & Ruxton (2002), suggesting a strong link between year-class strength and survival of early larval stages in February (and not March). Unfortunately, we only had otoliths from 3 years in our possession. A more complete comparison of the timing of first feeding and recruitment was therefore not possible. A comparison of the oceanographic conditions within the first-feeding period each year (instead of fixed windows, February and March) would also have been useful.
Utility of flow regime and other environmental descriptors in probabilistic forecasts

On several occasions, *Calanus finmarchicus* has been highlighted as an important indicator of sandeel recruitment (Arnott & Ruxton 2002, van Deurs et al. 2009, Lindegren et al. 2018). This link is based on correlations between *C. finmarchicus* abundance in February and sandeel recruitment, and has been explained by the potential naupliar production in February, when the overall zooplankton concentration is at its lowest (Arnott & Ruxton 2002). However, the present study revealed that, while the 2 best *C. finmarchicus* years coincided with good recruitment years, other recruitment spikes occurred in very poor *C. finmarchicus* years (i.e. 1996). In comparison, recruitment never occurred outside a negative flow regime in February. These findings suggest that sandeel larvae do not rely entirely on *C. finmarchicus* for survival, as previously hypothesized. Instead, it may be that sandeel recruitment and the retention of *C. finmarchicus* near the DB are both favoured by a negative associated flow regime. Planque & Batten (2000) explained the very low number of *C. finmarchicus* recorded by the CPR in the North Sea in 1996 by the fact that there was an unusually small *C. finmarchicus* population in the same year in the North Atlantic. However, it is counterintuitive that distinct *C. finmarchicus* spikes occur in negative flow regimes, given the consensus hypothesis that *C. finmarchicus* drift in a south-easterly direction into the North Sea in the first quarter of the year through the Orkney-Shetland channel and the Norwegian trench (Gallego et al. 1999, Madden et al. 1999). One plausible explanation could simply be that the surface water flow in the central North Sea is largely disconnected from the deep inflow events (below 150 m) responsible for transporting *C. finmarchicus* into the North Sea (Reid et al. 2003, Jónasdóttir & Koski 2011). Reid et al. (2003) also showed that the deep water inflow (<150 m) is negatively correlated to the inflow in the upper water column (0–150 m). Hence, the correlation between surface flow on top of the DB and deep inflow events is likely to be weak. Recently, Régnier et al. (2017) presented *C. helgolandicus* as a more important copepod species in relation to the year-class strength of sandeel west of the DB. This is with good reason, as *C. helgolandicus* has become the dominant *Calanus* species in the North Sea in recent decades, presumably due to climate change (Fromentin & Planque 1996, Hinder et al. 2014). However, in relation to the DB, we found no matches between years with large numbers of *C. helgolandicus* and years with good sandeel recruitment.

Why did SST and NAO coincide poorly with recruitment in the present study, when previous studies have shown significant relationships in time-series correlations (Arnott & Ruxton 2002, Lindegren et al. 2018)? The explanation regarding SST may already have been provided by Lindegren et al. (2018), who described how SST defines the recruitment trends, but not the extreme recruitment events. Therefore, while SST could potentially be used to inform managers about productivity regimes (Claussen et al. 2018, Lindegren et al. 2018), it has little value in relation to short-term forecasts of fishing opportunities, in particular for stocks displaying boom-and-bust dynamics (Stocker & Hilborn 1981, de Moor et al. 2011). NAO has been linked to *C. finmarchicus* regimes on a decadal time scale (Planque & Taylor 1998, Heath et al. 1999), and some degree of correlation between sandeel recruitment and winter NAO has also been reported (Arnott & Ruxton 2002). NAO influences the North Sea circulation usually with a positive relationship, where stronger westerly winds amplify the general cyclonic circulation during NAO+ phases. Nonetheless, positive phases also seem to favour wind conditions that could lead to circulation reversals on weekly and monthly scales (Mathis et al. 2015), which limits the chance of finding any robust correlations between NAO and local circulation patterns at the DB. It is therefore not surprising to find that NAO is a poor predictor of the inter-annual variation in sandeel recruitment.

As mentioned above, all good recruitment events coincided with a negative flow regime in February. In contrast, when a positive flow regime is observed in February, the prediction is that the recruitment will always be moderate to low. However, 3 out of the 7 years (1991, 2007, and 2010) assigned to the cluster of negative flow regimes in February were not good recruitment years. In this respect, it is important to mention that 1991 and 2007 represent peaks in the recruitment time-series, although they did not classify as ‘good recruitment’ years under the criteria set in our study. Furthermore, although 1991 had a flow trajectory almost identical to that of other good recruitment years, it also showed a unique signature of total stagnation in March, which could explain why good recruitment failed to take place in 1991 despite suitable conditions in February (i.e. assuming that stagnation is suboptimal for larval growth and survival). The year 2007 was characterized by a low spawning biomass (less than the time-series average minus 1 SD), suggesting some influence from the S-R relationship. Strong density-dependent regulation induced by 1 yr old fish in the population has been
proposed in former studies (e.g. van Deurs et al. 2009, Lindegren et al. 2018). Numbers of age-1 fish were about average or below in 1991 and 2007. However, in 2010 the second highest number of age-1 fish in the study period was recorded, potentially explaining the poor recruitment in this year (time-series of spawning stock biomass and numbers of age-1 fish are available in ICES 2016b).

**A recruitment hypothesis**

While the consensus in the literature regarding sandeels is that they appear to have strong links with specific prey types, coupling the ‘match–mismatch’ hypothesis (Cushing 1969, 1975, 1990) to mainly the relative large *Calanus* copepods advected into the North Sea (e.g. Arnott & Ruxton 2002, Régnier et al. 2017), we suggest considering alternative hypotheses, such as the ‘weak link/strong filter’ hypothesis proposed by Runge (1988), or the ‘Stable Ocean’ and ‘Optimal Environmental Window’ theories (Lasker 1988, or the ‘Stable Ocean’ and ‘Optimal Environmental Window’ theories (Lasker 1988, Cury & Roy 1989). Applying these to the sandeel case would imply that the link to *Calanus* copepods is relatively weak, and that the inter-annual variability of sandeel recruitment is instead filtered by smaller copepod species and other microzooplankton and strong links to the local physical environment, defining the small-scale trophodynamics experienced by the fish larvae. Previous reports of diet shifts in sandeel larvae to match available prey (de Figueiredo et al. 2005, 2007) and a connection between the timing of the peak in sandeel larvae abundance and the onset of phytoplankton production (Sherman et al. 1984, Monteleone & Peterson 1986, Malzahn & Boersma 2009) are in support of this hypothesis, because trophic flexibility and tight bonds to primary production disfavour a strong link to specific prey types, such as *Calanus*.

The present results not only indicate a strong link to the physical environment, but also suggest the importance of the sequence of favourable and unfavourable oceanographic conditions taking place within a critical recruitment window. For example, in the occasional year where favourable conditions are already established at the beginning of February, a whole month is added to the critical recruitment window, which in a ‘normal’ year does not start until March, where environmental conditions are much more stable from year to year (Wright & Bailey 1996, Lynam et al. 2013, Régnier et al. 2017). Therefore, the longer the sequence of favourable oceanographic conditions is, the larger is the recruitment (Fig. 7).

If favourable oceanographic winter (February) conditions occur often enough, early hatching may even be favoured, as it extends the duration of the growth period and increases the probability (relative to larvae hatching in March or April) that the critical threshold size is reached before winter (van Deurs et al. 2011). Studies on the yolk sac period in sandeel may support to this view. The yolk sac provides nutrition for sandeel larvae during the first ~12 d after hatching (Wright 1993), which helps them cope with low food availability for as much as 2 wk (Buckley et al. 1984, Régnier et al. 2017). At the same time, all winter-hatching sandeels are apparently capable of feeding prior to yolk sac absorption (Yamashita & Aoyama 1985), enabling advantageous utilization of an extended growth period whenever oceanographic conditions are already favourable in February.

The remaining question is: What does ‘favourable oceanographic conditions’ mean? In the search for direct causal relationships, we suggest that larval retention and advection processes on the DB are important. The flow regimes associated with unusually strong year-classes are characterized by either bidirectional flow or relatively limited net flow in a northerly direction in February (in contrast to a relatively strong net flow in a southerly direction, which prevails in most years). We hypothesize that this flow regime promotes dominance of southern water masses (e.g. from the Southern Bight, German Bight, and Wadden Sea), where primary production is highest in February (Joint & Pomroy 1993, Moll 1998). At the same time, the relatively limited net flow over the DB ensures larval retention and concentrates microzooplankton and phytoplankton for the early hatching larvae to feed on (Malzahn et al. 2007, Malzahn & Boersma 2009). These speculations are in line with earlier model simulations identifying the optimal sandeel hatching time to be February in the southeastern North Sea (Gurkan et al. 2013) and the DB to be a location where retention dominates over advection, facilitating perfect conditions for accumulating food and retaining sandeel larvae near suitable settlement habitats (Christensen et al. 2008).

Despite our efforts to identify and discuss possible causal relationships, the underlying mechanisms remain unclear, and the data presented here were not designed to support strong conclusions about anything other than the striking concurrence between unusually strong sandeel year-classes and negative flow regimes. We therefore encourage further research, pursuing the hypotheses and ideas developed in this study.
Conclusions and prospects of using oceanographic data to forecast stock productivity

Here we have demonstrated, for the first time, how internal North Sea circulation patterns can be used to predict fish recruitment in the North Sea. We found that good sandeel recruitment occurred only when negative flow regimes prevailed in February (and is most likely to occur in the 'retention' type of negative flow regimes). It is also plausible that these negative flow regimes can be translated into reversals of the predominant North Sea circulation pattern (i.e. changed from clockwise to counterclockwise), although this may be a rather oversimplified description of complex oceanographic processes, requiring further validation studies using, for example, North-Sea-wide 2D flow fields. Moreover, other candidate drivers, such as chlorophyll (Bakun 2006), might provide further insight into the mechanistic understanding behind these large year-classes. We also found indications of a previously unnoticed oceanographic regime shift in

Fig. 7. 'Recruitment window' hypothesis. Vertical grey arrows signify the order of events in the flowchart. The recruitment window represents the critical period where hatching and first feeding larvae are present. Within this window, it is the sequence of oceanographic events (i.e. flow regimes) that determines growth and survival of the larvae (i.e. flow regimes define the foraging arena and/or larval retention processes). For example, a given sequence can be comprised of both optimal conditions (labelled 'A') and poor conditions ('B'), where poor conditions lead to dramatically impaired survival (i.e. ≤10% of the survival experienced when conditions are optimal; see Houde 2008 regarding the scaling of larval mortality). In the flow chart, the different types of flow regimes found in the present study are used to exemplify optimal and poor conditions (illustrated with arrows and labelled A & B). Note that in stagnant flow regimes (flow regime on the far right) it is unclear from the present results whether this translates into optimal or poor conditions for the larvae. In the end, total recruitment is approximately proportional to the ratio between optimal and poor conditions within the recruitment window.
the North Sea taking place around 2002, which also warrants further investigation. Lastly, we recognise that a relatively coarse resolution in ocean models (such as in the model used here) can lead to an under-estimation of the volume transport, making it easier for wind forcing to affect surface flow (Påtsch et al. 2017). Hence, we recommend that future studies use a higher horizontal model resolution.

The use of oceanographic data in recruitment forecasts is still very limited (e.g. Myers 1998, Payne et al. 2017), despite the fact that oceanographic and meteorological data have proven useful in understanding recruitment dynamics of some of the largest fish stocks in the world. For example, there is a link between productivity of Pacific sardine and wind-driven upwelling systems off the coast of Central America and coupling between certain physical conditions of the Norwegian Coastal Current and the survival and growth of Norwegian spring spawning herring larvae drifting toward the nursery grounds in the Barents Sea (Rykaczewski & Checkley 2008, Skagseth et al. 2015). In this study, we have demonstrated that information about local flow regimes out-performs other previously considered recruitment predictors with respect to forecasting the most extreme recruitment events. Our approach differs from many other time-series studies of fish recruitment by being probabilistic (i.e. the RR approach) and focussing on the anomalies (i.e. the most extreme recruitment events) rather than on the average trends. This approach may be useful in regions with highly variable oceanographic conditions. Lastly, we propose a hypothesis for sandeel recruitment and its relation to physical oceanography, which we hope will inspire future research (Fig. 7).

While our study has quantified a probabilistic link between flow conditions and recruitment, there are additional considerations which must be addressed before such a relationship can be applied in stock forecasting. These include verification of the proposed recruitment hypothesis and a demonstration that such a forecast will effectively improve the stock advice with respect to forecast accuracy and stakeholder needs.

Acknowledgements. The contributions by M.v.D., S.J., and B.R.M. in this investigation were supported in part by the COFASP ERA-NET partners, which has received funding from the European Union’s Seventh Framework Program for research, technological development, and demonstration under grant agreement no. 321553 (GOFORIT project), and by the national funding agency of Denmark. M.v.D., O.H., and A.C. were supported by the European Fisheries Foundation (33113-B-16-080). Lastly, we thank 3 anonymous reviewers for providing very constructive and helpful feedback.

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Appendix. Additional information on the PCA

Fig. A1. Scree plots of eigenvalues ordered from largest to the smallest; (A) February, (B) March. The number of principal components (PCs) is determined at the point beyond which the remaining eigenvalues are all relatively small and of comparable size. Black bars signify PCs retained for PCAs.

Fig. A2. Correlation circles (A, February; B, March) showing correlations between years and principal components, PC1 (i.e. Dim1) and PC2 (i.e. Dim2), where correlated years are grouped together. The distance between arrows and the origin measures the quality of the years on the factor map. Variables that are away from the origin are well represented on the factor map.
Fig. A3. Total contribution of years to principal components PC1 and PC2 in February and March. Contributions of variables in accounting for the variability in a given PC are expressed in percentage (%). The red dashed line on the graph indicates the expected average contribution.
Scale-specific density dependence in North Sea sandeel

Rindorf, A., Henriksen, O., & van Deurs, M.

*Marine Ecology Progress Series*

619, 97-110, 2019

DOI: https://doi.org/10.3354/meps12945
Scale-specific density dependence in North Sea sandeel

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Published in:
Marine Ecology - Progress Series

Link to article, DOI:
10.3354/meps12945

Publication date:
2019

Document Version
Peer reviewed version

Link back to DTU Orbit

Citation (APA):
Scale-specific density dependence in North Sea sandeel

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Abstract

Density dependent demographic processes occur in many marine fishes and potentially enhance the stability of local aggregations and regional populations. The degree of density dependence exhibited at the population level is a combination of local density dependent effects acting on different spatial scales. In this study, we searched for density dependence in recruitment, growth, and mortality of North Sea sandeel \textit{Ammodytes marinus} at different spatial scales by analysing data at a spatial resolution specifically reflecting the mosaic of populated habitat patches. Two types of density dependent processes occurred: A shift in the spatial distribution towards low mortality areas when overall recruitment level was high and an increase in local mortality as local density increased. When combined, these processes largely compensated for each other and the size of the overall population had little influence on population level mortality. The study points to
the necessity of considering both local and regional scale processes in analyses of density dependence.

**Key words**
Spatial scale-dependency, density dependent distribution, demographic processes

**Introduction**
Density dependent demographic processes are thought to be an essential mechanism ensuring stability, resilience, and persistence in marine fish populations, which often experience large temporal variability in productivity (Turchin 1999, Berryman et al. 2002, Lande et al. 2002). However, demonstrating density dependence in marine fish populations is challenging (Hixon et al. 2002). The challenges may relate to the open dispersive phase, that decouples local reproduction and subsequent recruitment of juveniles to the population (Webster 2003) and the fact that marine processes are difficult to observe and hence, the available data are often confounded by high variance and potential bias (Hixon & Carr 1997). An additional issue may be the mismatch between the spatial scale of population studies and the scale at which density dependent mechanisms act (Shima & Osenberg 2003, Melbourne & Chesson 2005, Einum & Nislow 2005). This mismatch could explain why studies of density dependence in reef-associated species with well-defined habitat boundaries and high local densities often reveal significant results (Anderson 2001, Rose et al. 2001, Hixon & Jones 2005), whereas effects of density dependence in species with more open population boundaries are less frequently detected (Myers
Further, if the distribution of individual fish is density dependent (e.g. MacCall's basin theory, MacCall 1990), the combined effects of local density, local mortality and distribution can result in density dependence at population scale which differs substantially from that observed at local scale (Shima & Osenberg 2003).

Sandeels *Ammodytes spp.* form an important link between lower and upper trophic levels in many shelf ecosystems (Hedd et al. 2006, Frederiksen et al. 2006, 2007, Eliasen et al. 2011). They are entirely dependent on coarse sandy sediments as they spend a considerable part of their non-feeding periods buried (Winslade 1974a, b, c). The pelagic larvae can be transported considerable distances by currents before settling into sandy habitat (Potter & Lough 1987, Proctor et al. 1998) but the exchange of post-settled sandeels between the sandy habitat patches is low (Jensen et al. 2011). The high site fidelity after settling into fragmented habitat combined with large fluctuations in densities (Wright et al. 2000, Holland et al. 2005) makes the lesser sandeel *Ammodytes marinus* in the North Sea an ideal case for investigating the effect of density dependence on population dynamics. Previous studies of the North Sea lesser sandeel have indicated the existence of density dependent processes at a regional scale (Arnott & Ruxton 2002, van Deurs et al. 2009), acting concurrently with predation mortality, fishing pressure and climatically-induced changes in prey abundance to determine population size (Clausen et al. 2017, Lindegren et al. 2018). However, these studies did not investigate the role of density dependence acting within local habitat patches.

In the present study, we hypothesize that: (1) the spatial distribution of recruitment measured by the catch rate of 1-year old fish depends on regional density in a given year, (2) local recruitment depends on local density the previous year, (3) density dependent mortality occurs at a local scale.
and (4) the cumulated effect when scaling up to population level differs from the processes acting on a local scale. To investigate these hypotheses, we used a series of statistical models to analyse density dependent recruitment and mortality, taking into account both local and regional densities. The analysis was based on catch rates of lesser sandeel (*Ammodytes marinus*) in the North Sea commercial sandeel fishery and in a scientific survey at Shetland.

**Materials & methods**

**Data**

The majority of the data was derived from a self-sampling programme on commercial sandeel fishing vessels. Vessels in the programme recorded the exact location and time of shooting and hauling of the trawl, and an estimate of the total weight of the catch in each individual haul. A sample of 0.5 to 1 kg fish was collected from each haul and frozen on board. In the laboratory, the lesser sandeel were length measured to nearest half cm below (Rindorf et al. 2016). Samples were assigned to fishing grounds based on the distance between the midpoint of the haul and the nearest fishing ground (Jensen et al. 2011) and hauls with midpoints closer than 1 km to a fishing ground were assumed to be taken on that fishing ground. All fishing grounds were located in the North Sea between 54°N and 57°N (fig. 1) and all participating vessels were Danish. The collection of samples started in 1999 with between 8 and 29 vessels participating each year (on average 15) until 2014, where the number of vessels increased to between 31 and 58 (on average 44). In 2012 and 2016, the fishery was restricted to a monitoring fishery in April before the main fishing season, and hence not strictly comparable to the catch rates from the remaining years. These years were therefore excluded from the analyses.
In addition to the commercial data described above, data from a scientific survey conducted at Shetland from 1985 to 2000 were also included (Cook 2004). During this period, sandeel at Shetland were subject to zero or very low fishing pressure and the data were therefore used to study the relationship between density and natural mortality. Data on regional stock size was derived from agreed sandeel assessments (ICES 2018).

Catch rate in numbers at age \( a \) per minute fishing \((C_a, \text{in units of sandeels caught min}^{-1})\) was estimated by combining estimated catch in kg per minute fishing with numbers per kg of each age group. The latter was estimated by applying separate age-length keys for each fishing ground and week where possible; otherwise data from within the same statistical rectangle (1°W times 0.5°N) and two consecutive weeks were combined before fitting the age-length key. The age-length key analysis used the method described in (Rindorf & Lewy 2001). In some hauls, the number of large fish was too low to provide reliable estimates of the number of fish older than age 1. Hence, the number of data values for age 1 exceeded that for age 2.

To avoid violating assumptions of the statistical regression models used, a sequence of transformations and statistical modelling was used. First, the variance of catch rates tends to increase with the mean (Pennington 1983). To address this, all catch rates were transformed by taking the natural log. Secondly, if the error of the independent variable is in the same order of magnitude as that of the dependent variable, parameter estimates in standard regression models may be considerably biased (Kendall & Stuart 1979). This problem was addressed by using average catch rates across all samples in a given year whenever catch rates were used as an independent variable. This decreases the standard error of the independent variable compared to that of the dependent variable. Thirdly, the sampling design was highly unbalanced and using mean catch
rates as the dependent variable in a standard linear regression would violate the assumption of
constant variance of the observations. We used individual catch rates as observations in all
analyses to accommodate the unbalanced sampling design and to assure that the variance of the
dependent variable is considerably larger than that of the independent variable. Lastly, the data
from a specific fishing ground, fishing vessel, or year are likely to be correlated due to e.g. local
weather effects, skipper skills etc. To address this, random effect models were used throughout
and the r² of the model using only fixed and both fixed and random effects given (Nakagawa &
Schielzeth 2013).

Spatial distribution of recruitment depends on regional density in a given year

(Hypothesis 1)

The relationship between spatial distribution of recruitment measured by the catch rate of 1-year
old fish and density in the given year was investigated by relating the catch rates of 1-year old
sandeel on the individual fishing grounds to that of a central reference ground. This will reveal if
different grounds experience the same relative (regional) annual change in recruitment or if some
grounds exhibit greater changes than others. The analysis was performed using a random effects
model, where the central well-sampled fishing ground, North West Rough, was used as the
reference ground and catch rate of 1-year old fish was used as recruitment proxy:

\[
\ln \hat{C}_{1,g,y,v} = k_g + y_g \ln \bar{C}_{1,NW Rough,y} + \omega_{g,y} + \varphi_v
\]  

(1)

Here, \( \ln \hat{C}_{1,g,y,v} \) is the predicted log catch rate of 1-year olds of vessel \( v \) at fishing ground \( g \) in year \( y \), \( \ln \bar{C}_{1,NW Rough,y} \) is the average log catch rate of 1-year olds on North West Rough in the given
year and \( k_g \) is the theoretical catch rate at fishing ground \( g \) when \( \ln \bar{C}_{1,NW Rough,y} \) is 1. The slope \( y_g \)
describes the fishing ground specific relationship with density at the reference ground and the
random effects of year/fishing ground and fishing vessel ID are contained within $\omega_{g,y} \in N(0,\sigma_\omega)$ and $\varphi_v \in N(0,\sigma_\varphi)$, respectively. If $g$ is close to one and $\sigma_\omega$ and $\sigma_\varphi$ are small, virtually all variation is explained by the recruitment at the reference ground, North West Rough (no density dependence). If $g$ values $> 1$, there is positive density dependence at the fishing ground, and an increased recruitment on the reference ground is accompanied by a higher than proportionally increased recruitment at other grounds. In contrast, $g$ values between 0 and 1 are indicative of negative density dependence at the fishing grounds, where an increased recruitment on the reference ground is accompanied by a lower than proportionally increased recruitment at other grounds. Lastly, if $g$ is close to zero and $\sigma_\omega$ and/or $\sigma_\varphi$ are large, the development in local recruitment is independent of that recorded at the reference ground. Since $g$ is estimated for each fishing ground, it is possible that negative density dependence is detected on some grounds and positive density dependence on others. The model was fitted to all data as well as to a subset of data consisting only of fishing grounds within sandeel population area 1 (fig. 1). A similar model was made for population area 4 (fishing grounds close to the coast of Scotland, fig. 1) using Berwick Bank as the reference fishing ground. The areas are considered to contain separate populations (ICES 2016) and hence correlation is expected within areas but not necessarily between areas.

If recruitment to different fishing grounds is density dependent, the economic profitability of different fishing grounds may vary with density leading to a relationship between catch rates and stock size that differs from proportional at the regional scale (density dependent catchability). In order to test for density dependent catchability at the regional level, the yearly average catch
rates of age 1 sandeel were compared to the number of age 1 fish on January 1st estimated in the
analytical assessment (ICES 2018) using a log-linear model:

\[
\ln \hat{C}_{1,g,y,v} = k_g + \eta_g \ln R_{1,y} + \omega_{g,y} + \phi_v \quad (2)
\]

where \( \hat{C}_{1,g,y,v} \) is the predicted catch rate of age 1 sandeel of vessel \( v \) at fishing ground \( g \) in year \( y \),
the constant \( k_g \) represents the average catch rate at the fishing ground at a theoretical abundance
of 1 (not related to \( k_g \) in eq. 1), \( R_{1,y} \) is number of age 1 fish on January 1st in year \( y \) taken from the
analytical assessment, and \( \eta_g \) describes the ground-specific dependence of catch rates on \( R_{1,y} \).

\( \omega_{g,y} \sim N(0, \sigma_\omega) \) describes the random effect of year and fishing ground and \( \phi_v \sim N(0, \sigma_\phi) \)
describes the random effect of vessel ID. For catchability to be density independent, \( \eta_g \) must be
one. If \( \eta_g \) is larger than one, catch rates decrease faster than proportionally as abundance
decreases (hyperdepletion, (Hilborn & Walters 1992)). If \( \eta_g \) is less than one, catch rates decrease
slower than proportionally as abundance decreases (hyperstability, (Hilborn & Walters 1992)).

Temporal trends in catchability at age 1 was analysed by making \( \eta_g \) a linear function of year and
testing whether this improved model fit significantly.

Local recruitment depends on local density the previous year (Hypothesis 2)

Recruitment can be temporally density-dependent if the recruitment on a given fishing ground in a
given year depends on the recruitment to that specific ground in the preceding year. This type of
density dependent recruitment was tested using the following model:

\[
\ln \hat{C}_{1,g,y,v} = k_y + \kappa_g \ln \hat{C}_{1,g,y-1} + \omega_{g,y} + \phi_v \quad (3)
\]
Here, \( \ln \hat{C}_{1,g,y,v} \) is still the predicted log catch rate of 1-year olds of vessel \( v \) at fishing ground \( g \) in year \( y \) and \( \ln \hat{C}_{1,g,y-1} \) is log catch rate of 1-year old fish (used as a proxy for recruitment) for a given fishing ground in the preceding year (\( y-1 \)). The intercept \( k_y \) describes the predicted catch rate at a theoretical average recruitment in the preceding year equal to 1, \( \kappa_g \) describes the effect of the recruitment in the preceding year and the random effects of year/fishing ground and fishing vessel ID are again contained within \( \omega_{g,y} \in N(0, \sigma_\omega) \) and \( \varphi_v \in N(0, \sigma_\varphi) \), respectively. Note that the density dependent effect was estimated for each fishing ground separately.

Density dependent mortality occurs at local scale (Hypothesis 3)

The density of a cohort will decrease exponentially from year \( y \) to year \( y+1 \) as fish are removed by mortality, according to the population decay function:

\[
N_{a+1,y+1} = N_{a,y}e^{-Z_y}
\]

Where \( N_{a,y} \) is the number of fish in the population of a given age class \( a \) at the beginning of the year \( y \) and \( Z_y \) denotes the total mortality rate for a given year. Using catch rates as indicators of abundance, we can adapt the above equation:

\[
\hat{C}_{2,y+1} = \frac{q_{2,y+1}}{q_{1,y}} \hat{C}_{1,y}e^{-Z_y}
\]

Hence, if the relative difference in catchability of the two age groups and mortality remain constant over time, the catch rate of a given cohort in a particular year is directly proportional to the catch rate of the same cohort in the preceding year. Note that when we use catch rates rather than abundance, catch rates of e.g. 2-year olds (\( C_2 \)) may exceed that of 1-year olds (\( C_1 \)) the year
before if catchability of 2-year olds ($q_2$) is higher than of 1-year olds ($q_1$). If mortality is density
dependent, $Z_y$ is a function of the population density in that year. Assuming that mortality is
linearly related to log abundance with the proportionality factor $\beta$, this relationship can be
described as:

$$Z_y = Z_0 + \beta \ln N_{1,y} = Z_0 - \beta \ln q_{1,y} + \beta \ln \hat{C}_{1,y}$$

Where $Z_0$ is the theoretical mortality at $\ln \hat{C}_{1,y} = \ln q_{1,y}$ or $\beta = 0$. When inserting this relationship
and taking the natural logarithm on both sides, we get

$$\ln \hat{C}_{2,y+1} = k_{y+1} + (1 - \beta) \ln \hat{C}_{1,y}$$

where $k_{y+1} = \ln \left( \frac{q_{2,y+1}}{(q_{1,y})^{1-\beta}} \right) - Z_0$.

Estimates from the stock assessment of sandeel in area 1 indicate that the ratio $\frac{q_2}{q_{1,y-1}}$ is increasing
over time (ICES 2018), and this was accounted for in the model based on the equation above:

$$\ln \hat{C}_{2,g,y+1,v} = k_0 + k_1 y + (1 - \beta_g) \ln \hat{C}_{1,g,y} + \omega_{g,y} + \varphi_v$$  \(4\)

where $k_0 = \ln \left( \frac{q_{2,2000}}{(q_{1,1999})^{1-\beta}} \right) - Z_0$, $k_1 = \Delta \ln \left( \frac{q_2}{(q_1)^{1-\beta}} \right)$ describes the annual change in the ratio of
catchabilities, $\beta_g$ describes the density dependent effect of last year’s geometric average catch
rate of 1-year olds, $\ln \hat{C}_{1,y}$, on mortality at fishing ground $g$, allowing us to determine if mortality
differs between high and low survival grounds as suggested by Shima and Osenberg (2003).

Random effects of year/fishing ground and fishing vessel ID are again contained within $\omega_{g,y} \in N(0, \sigma_\omega)$ and $\varphi_v \in N(0, \sigma_\varphi)$, respectively. Mortality is independent of density when $\beta = 0$. If $\beta$ is
greater than zero, mortality increases with density. $\beta$ was estimated at the two fishing grounds
with 8 or more years of data (North West Rough and Southernmost Rough). Due to the very limited catches of fish of age 3 and older, only mortality from 1-year olds to 2-year olds was investigated. To allow comparison of mortality levels between fishing grounds, mortality indices for fishing grounds with at least 5 years data were estimated assuming $\beta = 0$ as $\ln \tilde{C}_{2,y+1} - \ln \tilde{C}_{1,y}$.

Catch rates from a scientific survey around Shetland was analysed using a slightly different model without random effect terms and time trend in catchability:

$$\ln \tilde{C}_{a+1,y+1} = k_0 + (1 - \beta) \ln \tilde{C}_{a,y}$$

These simplifications were required since only one value per year was available and it is reasonable to assume that catchability in a scientific survey is constant over time. More ages were available than in the commercial samples and the analysis therefore included ages 0 to 4. Since $\ln \tilde{C}_{a,y}$ is observed with error, ordinary regression is not appropriate. Instead, Deming regression was used to estimate $\beta$ assuming the error in the dependent and independent variable to be equal (Linnet 1993). The 95% confidence limits of $\beta$ were estimated using jackknife.

Cumulated density dependent effects differ from the processes acting on a local scale (Hypothesis 4)

Following the analyses of density dependence in recruitment and mortality, the predictions from the two analyses were combined to assess the integrated effect of local density dependence in mortality and spatial distribution of recruitment on regional mortality (summed across local fishing grounds). Three different combinations were examined:
1. Spatial distribution of recruitment depends on regional density and local mortality is independent of local density

2. Spatial distribution of recruitment is independent of regional density and local mortality depends on local density

3. Spatial distribution of recruitment depends on regional density and local mortality depends on local density

For options one and three, an index of abundance at each fishing ground, $I_g$, was estimated as the product of local density estimated from the relationship with density at North West Rough and the surface area of the fishing ground, $A_g$:

$$I_{1,g,y} = A_g e^{(k_g + \gamma_g \ln C_{1,NWRough,y})}$$

Where $k_g$ and $\gamma_g$ are estimated in model 1. For option 2, the ground specific index of abundance was estimated as the ground specific median abundance index multiplied by area of the ground.

As the aim is to investigate the impact of the each of the density dependent components distribution and mortality, the observed abundance at age 2 cannot be used as this includes both effects. Instead, the index of abundance of 2-year old fish at each ground for this analysis was estimated as $I_{2,g,y} = I_{1,g,y} \exp(-Z_{1,g,y})$. For option 1, the average mortality index at each ground, $Z_{1,g,y}$, was assumed equal to the observed $k_{0,g} = \ln C_{a+1,y+1,g} - \ln C_{a,y+1,g}$ averaged across years. For options 2 and 3, the annual mortality index at a ground was assumed equal to $k_{0,g} - \beta \ln C_{a,y+1,g}$ where the value of $\beta$ was estimated in model 4.

The total mortality index across fishing grounds was estimated as:
\[ Z_{\text{pop},y} = \ln \left( \sum_g I_{1,g,y} \right) - \ln \left( \sum_g I_{2,g,y} \right) \]

This was compared to an index of total abundance of age 1 fish across fishing grounds estimated as:

\[ I_{\text{pop},y} = \ln \left( \sum_g I_{1,g,y} \right) \]

As the abundance and mortality are indices rather than absolute values, both are given relative to the value at median density.

Results

Spatial distribution of recruitment depends on regional density in a given year (Hypothesis 1)

The fixed effects model for fishing grounds in assessment area 1 explained 57% of the variation, and the combined fixed and random effects explained 66% (fig. S1 in supplementary material). The standard deviation of the random effect of fishing ground and year (0.31) was much larger than that of vessel ID (0.18), but smaller than the residual deviation (1.84). The fishing ground Lisborgs Revle had a slope \( (\gamma_g) > 1 \) (table 2). The remaining fishing grounds in assessment area 1 showed no significant difference in \( \gamma_g \) (P=0.6031). The joint slope at these grounds was 0.62 (table 3), which was significantly different from both 0 and 1 (P<0.001 in both cases). Hence, when recruitment at age 1 increased by 100% at North West Rough, recruitment at Lisborgs Revle increased by 155% and recruitment at fishing grounds other than Lisborgs Revle increased by only 54% (fig. 2). These
density dependent differences in catch rates across grounds meant that when catch rates were low on average across all grounds (i.e. low regional population density), North West Rough and Lisborgs Revle catch rates were low relative to other grounds, while catch rates at these grounds were the highest observed when average catch rates were high (fig. 3). In spite of these differences, strong year-classes were detectable across all grounds as above average densities, while weak year-classes provided below average densities across all grounds (i.e. note the difference in scale in fig. 2).

Annual recruitment at fishing grounds in assessment areas 2 and 4 was not related to catch rates at North West Rough ($γ_g$ not different from zero, $P=0.0604$, fig. 3). However, catch rates at Wee Bankie were significantly related to those at Berwick Bank (area 4, $P=0.0158$).

Catch rate in area 1 was highly correlated to abundance estimated from the analytical assessment ($P<0.0001$, $r^2$ of fixed and random effects together=59%, (fig. 4 and fig. S2)). The estimated slope ($η_g$) of the relationship between catch rate and abundance was 1.24 with a standard error of 0.13, not significantly different between fishing grounds ($P=0.3355$). The value is not significantly different from one ($P=0.0718$) and hence there was a non-significant tendency towards density dependent catchability at a population level. There was no significant trend over time in catch rate divided by stock abundance (i.e. index of catchability at age 1) ($P=0.1226$).

Local recruitment depends on local density the previous year (Hypothesis 2)

Recruitment at age 1 to a given fishing ground was not significantly related to the recruitment in the previous year ($P=0.1170$).
Density dependent mortality occurs at local scale (Hypothesis 3)

Only North West Rough and Southernmost Rough were sampled sufficiently to allow the estimation of density dependence in mortality while seven grounds were sampled sufficiently to allow the estimation of a ground specific mortality index (fig. 5 and 6). Among the seven grounds sampled, Lisborgs revle had the lowest mortality, S.W. Patch and Elbow Spit the highest while the remaining grounds had intermediate values. The catch rate at age 2 was highly related to catch rate of 1-year old fish (P<0.0001) and the model explained 51% and 65% of the variation by fixed and fixed plus random effects, respectively (fig. S3). The effect of year, $k_1$, was significantly positive (P=0.0364), indicating that catch rates at age 2 increased over time even if catch rate of 1-year old fish remained unchanged. $\beta$ was 0.19 and 0.21 at North West Rough and Southernmost Rough, respectively and neither $\beta$ nor $k_0$ differed between the two fishing grounds (P>0.0795). The joint density dependent term $\beta$ was significantly positive ($\beta$=0.21, std=0.09, P=0.0218). The model used for the Shetland data revealed a common $\beta$ of 0.27 (std=0.07), significantly greater than 0 (P=0.0003) (fig. 7). With this strength of density-dependence, the smallest average catch rate of 1-year olds at North West Rough resulted in a 230% higher catch rate when the fish were 2-year olds, corresponding to a higher catchability of 2-year olds compared to 1-year old fish masking the effects of mortality. In contrast, the largest average catch rate of 1-year olds at North West Rough resulted in 58% lower catch rate when the fish were 2-year olds, corresponding to an 8-time reduction in survival between the smallest and the largest year-class (assuming constant catchability at age). The density dependence at Shetland was sufficient to reduce the survival of the largest and smallest index by a factor 5. This could potentially be contributing to the stabilization of the population by increasing mortality of large year-classes.
Cumulated density dependent effects differ from the processes acting on a local scale

(Hypothesis 4)

While density dependent mortality led to increased mortality at higher densities (fig. 8, dark grey broken lines), density dependent distribution of recruitment to age 1 led to the opposite result, as the proportion of fish settling to recruit at age 1 at grounds showing high mortality decreased when the overall recruitment in the population was high (fig. 8, light grey dotted lines). Combining the two for fishing grounds in the Dogger Bank area resulted in a mortality index, which was virtually independent of abundance (solid black line in fig. 8). Excluding S. W. Patch, which had a very high estimated mortality index and a very large area, changed the result so the combined effect of density dependent recruitment and mortality was an increase in mortality with abundance, acting to decrease fluctuations in stock abundance at age 2 compared to age 1. If we assume that catchability of age 1 and 2 are equal, this corresponds to a reduction in survival from 47% at the lowest observed abundance to 18% at the highest observed abundance. The results of all density dependence investigations are summarised in table 4.

Discussion

The regional population processes of North Sea sandeel were a combination of density dependent spatial distribution of recruitment on a regional scale and density dependent mortality on a local scale. In years characterized by a large overall population, a large fraction of the population occurred at low mortality fishing grounds while local mortality increased. Depending on the
balance between these two factors, this potentially leads to either increasing or decreasing mortality as abundance increases.

Sandeel recruitment in all areas increased as overall recruitment increased, but the increase was substantially greater at North West Rough and Lisborgs Revle. Consequently, the relative contribution of these grounds shifted from supporting the lowest sandeel densities in years where the overall population size was small to supporting the highest densities when the overall population size was large. This density dependence in the distribution of recruitment across fishing grounds does not follow the most commonly referenced distribution hypotheses. For example, the basin theory (MacCall 1990) and the theory on cryptic density dependence (Shima & Osenberg 2003) predicts that high quality habitat is always occupied and exhibits the highest densities. This is not the case in our data, as the two grounds switch from having the lowest relative density to the highest relative density. Sutherland’s (1983) theory of fish distribution, based on a different parametrization of the Ideal Free Distribution (Fretwell & Lucas 1969), predicts that as the overall population size goes up, local densities throughout the population range increase proportionally. However, this prediction does not match our results either. An alternative explanation for our observations could be spatio-temporal variation in the environmental conditions for recruitment. If oceanographic features, such as advection and retention, vary in different years, this might affect recruitment of settling larvae by shaping the trophodynamic arena that regulate survival through food availability and the physical settings that determine transport into and retention within an area (Henriksen et al. 2018). For example, if the recruitment conditions such as food availability and drift pattern are highly variable in the northwest corner of Dogger Bank but more stable in other areas and large food availability only occurs in the northwest corner of Dogger Bank when there is a high food supply overall, this could explain the greater variation at North
West Rough and Lisborgs Revle. Alternatively, the number of sandeel dying from predation before age 1 in these two areas is a constant number rather than a constant fraction. This would lead to a greater mortality up to age 1 at low abundance than at high abundance and could be the result of a predator stock which remains approximately constant and is capable of feeding at approximately the same rate regardless of overall sandeel density (i.e. limited by handling time rather than search time (Stephens & Krebs 1986)).

The distribution of sandeel recruitment was not affected by the density of the previous cohort. This is in contrast to studies on sandeel abundances reporting negative correlations between the recruitment in a given year and that in the previous (Arnott & Ruxton 2002, van Deurs et al. 2009, Lindegren et al. 2018). It is possible that the residual variation in our data was too large for the density dependent effect to be detected at the local scale. Alternatively, the autocorrelation seen in earlier studies was caused by factors relating to the assessment model output used. If the commercial fishery targets fishing grounds with high abundance of specific cohorts, this can introduce an overrepresentation of these cohorts and an underrepresentation of the adjacent cohorts in the regional catch data, leading to the impression that there is negative autocorrelation at the population level, even though there is no autocorrelation at the local scale.

Density dependent mortality substantially reduced the difference between large and small local cohorts at the local level, potentially contributing to the stability of local aggregations. The density dependent mortality seemed to be a result of predation rather than fishing, as it was present at approximately the same level in unfished (Shetland) and fished areas (North West Rough and Southernmost Rough). Density dependent natural mortality of fish such as damselfish (*Dascyllus flavicaudus*) and bridled goby (*Coryphopterus glaucofraenum*) acts through exposing individuals to
higher predation rates once the carrying capacity of an area has been reached (Forrester & Steele 2004, Schmitt & Holbrook 2007). In the case of sandeel, carrying capacity may refer to the availability of suitable burying substrate rather than to refuges as in reef fish (Hobson 1986). Different substrates may offer different overwintering survival or increased food competition may lead to delayed onset of the overwintering period, increasing predation mortality (van Deurs et al. 2011). There was no significant difference in the level of density dependent mortality at the three sites examined, indicating that either the sites are similar in quality or the factors inducing density dependence are not related to quality of the sites as found for coral reef fish, such as Thalassoma Hardwicke (Shima & Ostenberg 2003).

Density dependence in natural mortality occurs if natural predators switch between different prey types according to their abundance, either by changing their consumption or by exhibiting an aggregative response (Murdoch et al. 1975, Anderson 2001). Large-scale studies of the diet of predatory fish in the North Sea and Celtic Sea have generally failed to produce evidence of more than proportional increases in consumption of individual predators with increasing prey density (Pinnegar et al. 2003, Rindorf & Gislason 2005, Rindorf et al. 2006). However, as areas of sandeel habitat are characterised by highly stationary features (gravelly substrate and limited depth range), they can potentially be targeted accurately by aggregating natural predators (Temming et al. 2004, van der Kooij et al. 2008, Engelhard et al. 2008). Hence, it is possible that extensions in the period in which the predators feed on sandeel and aggregation of predators in areas with high densities of sandeel lead to the observed density dependence of mortality from age 1 to 2.

If the fishery optimises revenue by seeking out the highest catch rates, the density dependent distribution of recruitment will lead to a widespread fishery with low catch rates and little fishing
activity at North West Rough and Lisborgs Revle when the overall population is small. When the population is large, the fishery will exhibit high catch rates and concentrate at North West Rough and Lisborgs Revle. This general pattern seems to be confirmed by the distribution of commercial catches in 2003-2005, where abundance was low compared to later years (ICES 2018). The generally reported form of density dependence of catch rates is hyperstability, where catch rates decrease slower than abundance (Saville & Bailey 1980, Winters & Wheeler 1985, Beverton 1990). This has been suggested to be a major cause of overfishing (Erisman et al. 2011). In contrast, the pattern in our data is likely to lead to hyperdepletion of catch rates, where catch rates decrease faster than fish abundance at a regional scale. This is also indicated by the analysis of density dependent catchability, where the slope ($\eta$) (eq. 2) was estimated to be 1.24, consistent with hyperdepletion. Alternatively, local catchability depends on local density. If this is the case, it would bias the analysis of density dependence of mortality. However, to produce the impression of mortality increasing with density where no such underlying process exists, catchability for age 1 must increase with density more than that of age 2. This is consistent with hyperdepletion for age 1 rather than the more commonly reported hyperstability. It is not clear by which process the catchability at a local fishing ground would increase with density. The opposite relationship, however, where catchability decreases with increasing stock size is consistent with fisheries targeting prime habitat into which the fish are aggregating to a greater degree when stock size is low.

In summary, the population dynamics of lesser sandeel in the North Sea rely on a mosaic of local habitats determining density dependence at the regional population level. Local density dependent mortality led to increasing mortality at higher densities. Concurrently, density dependent distribution of recruitment led to a shift in distribution towards low mortality fishing.
grounds when recruitment at the regional scale was high. As a result, hyperdepletion of catch rates was more likely than hyperstability. Combining the two density dependent effects for fishing grounds in the Dogger area resulted in a mortality index, which was virtually independent of abundance. Our study demonstrated the necessity of considering both local and regional processes in analyses of density dependence (Shima & Osenberg 2003, Einum & Nislow 2005): had the analysis considered only local density dependent effects on mortality, the conclusion of the study would have been in complete opposition to an analysis considering only density dependent effects on the spatial distribution of recruitment.

Acknowledgements

We are deeply grateful for the effort of the fishing skippers, who collected the data and placed them at our disposal, to the Danish Fishing Producers Organization and the Danish Pelagic Producers Organization that supported the work and to Stina B. S. Hansen and the laboratory technicians who worked up the thousands of length samples. The work was funded by the EMFF project ‘Forvaltningsmodeller for fiskebestande’ 33113-B-16-080.

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Table 1. Overview of models and density dependent terms used. In the following, $k$ is used to denote a constant in the specific model and hence, though $k$ appears in several models, the estimate of $k$ differs in each case.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Model</th>
<th>Density dependence analysed</th>
<th>Tests performed</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$\ln \hat{C}<em>{1,g,y,v} = k_g + \gamma_g \ln \hat{C}</em>{1,NWRough,y} + \omega_{g,y} + \varphi_v$ (1)</td>
<td>The regional effect of recruitment to North West Rough (used as reference fishing ground) on the recruitment to other fishing grounds.</td>
<td>$\gamma_g \neq 0$ $\gamma_g \neq 1$</td>
</tr>
<tr>
<td>1</td>
<td>$\ln \hat{C}<em>{1,g,y,v} = k_g + \eta_g \ln R</em>{1,y} + \omega_{g,y} + \varphi_v$ (2)</td>
<td>The regional effect of population abundance of age 1 fish on the catch rates of age 1 fish on the individual fishing grounds.</td>
<td>$\eta_g \neq 0$ $\eta_g \neq 1$</td>
</tr>
<tr>
<td>2</td>
<td>$\ln \hat{C}<em>{1,g,y,v} = k</em>{y,g} + \kappa_g \ln \hat{C}<em>{1,g,y-1} + \omega</em>{g,y} + \varphi_v$ (3)</td>
<td>Dependence of local recruitment in year $y$ on local recruitment in the</td>
<td>$\kappa_g \neq 0$ $\kappa_g \neq 1$</td>
</tr>
</tbody>
</table>
previous year to the same fishing ground.

| 3 | \(\ln\hat{C}_{2,g,y+1,v} = k_0 + k_1y + (1 - \beta_g)\ln\hat{C}_{1,g,y} + \omega_{g,y} + \varphi_v \) (4) | Dependence of local mortality on local cohort density. | \(\beta \neq 0\) |
Table 2. Parameter estimates of the model $\ln \hat{C}_{1,g,y} = k_{0,g} + \gamma_g \ln \hat{C}_{1,NW\text{Rough},y} + \omega_{g,y} + \varphi_v$ describing the relationship between catch rates of 1-year olds at North West Rough and other fishing grounds in assessment area 1. Significant probabilities (P) are in bold. N denotes number of observations used, Year denotes number of years where data were available from that fishing ground.

<table>
<thead>
<tr>
<th>Fishing ground</th>
<th>Ass. area</th>
<th>N</th>
<th>Year(s)</th>
<th>$\gamma_g$</th>
<th>P($\gamma=0$)</th>
<th>$k_{0,g}$ in reduced model</th>
<th>$\gamma_g$ in reduced model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lisborgs Revle</td>
<td>1</td>
<td>313</td>
<td>11</td>
<td>1.35 (0.13)</td>
<td>&lt;0.0001</td>
<td>-4.07 (1.12)</td>
<td>1.35 (0.12)</td>
</tr>
<tr>
<td>Stenkanten</td>
<td>1</td>
<td>124</td>
<td>11</td>
<td>0.74 (0.10)</td>
<td>&lt;0.0001</td>
<td>3.15 (0.41)</td>
<td>0.62 (0.04)</td>
</tr>
<tr>
<td>Rute 18</td>
<td>1</td>
<td>61</td>
<td>7</td>
<td>0.72 (0.13)</td>
<td>&lt;0.0001</td>
<td>2.88 (0.42)</td>
<td>0.62 (0.04)</td>
</tr>
<tr>
<td>Southernmost Rough</td>
<td>1</td>
<td>234</td>
<td>14</td>
<td>0.67 (0.09)</td>
<td>&lt;0.0001</td>
<td>3.61 (0.40)</td>
<td>0.62 (0.04)</td>
</tr>
<tr>
<td>S. W. Patch</td>
<td>1</td>
<td>169</td>
<td>11</td>
<td>0.49 (0.10)</td>
<td>&lt;0.0001</td>
<td>3.91 (0.39)</td>
<td>0.62 (0.04)</td>
</tr>
<tr>
<td>Sorel</td>
<td>1</td>
<td>115</td>
<td>7</td>
<td>0.78 (0.30)</td>
<td>0.0093</td>
<td>3.47 (0.47)</td>
<td>0.62 (0.04)</td>
</tr>
<tr>
<td>Outer Well</td>
<td>1</td>
<td>85</td>
<td>6</td>
<td>0.48 (0.17)</td>
<td>0.0057</td>
<td>4.05 (0.44)</td>
<td>0.62 (0.04)</td>
</tr>
<tr>
<td>Elbow Spit</td>
<td>1</td>
<td>220</td>
<td>10</td>
<td>0.62 (0.12)</td>
<td>&lt;0.0001</td>
<td>3.83 (0.43)</td>
<td>0.62 (0.04)</td>
</tr>
<tr>
<td>Tail End</td>
<td>1</td>
<td>94</td>
<td>8</td>
<td>0.55 (0.10)</td>
<td>&lt;0.0001</td>
<td>3.92 (0.41)</td>
<td>0.62 (0.04)</td>
</tr>
</tbody>
</table>
Table 3. Proportion of individuals found in the Dogger Bank area present at each fishing ground.

<table>
<thead>
<tr>
<th>Fishing ground</th>
<th>Area (km²)</th>
<th>Average $\ln \hat{C}<em>{1,y-1}$/$\ln \hat{C}</em>{2,y}$</th>
<th>Proportion of all at minimum density at North West Rough</th>
<th>Proportion of all at median density at North West Rough</th>
<th>Proportion of all at maximum density at North West Rough</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lisborgs Revle</td>
<td>250</td>
<td>0.59</td>
<td>0.000</td>
<td>0.030</td>
<td>0.129</td>
</tr>
<tr>
<td>N.W. Rough</td>
<td>593</td>
<td>1.28</td>
<td>0.018</td>
<td>0.192</td>
<td>0.367</td>
</tr>
<tr>
<td>Southernmost Rough</td>
<td>204</td>
<td>1.64</td>
<td>0.048</td>
<td>0.085</td>
<td>0.074</td>
</tr>
<tr>
<td>Stenkanten</td>
<td>216</td>
<td>1.79</td>
<td>0.023</td>
<td>0.060</td>
<td>0.062</td>
</tr>
<tr>
<td>S. W. Patch</td>
<td>1285</td>
<td>2.76</td>
<td>0.911</td>
<td>0.634</td>
<td>0.368</td>
</tr>
<tr>
<td>Hypothesis number</td>
<td>Density dependence analysed</td>
<td>Tests results</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-------------------</td>
<td>---------------------------------------------------------------------------------------------</td>
<td>----------------------------------------------------------------------------------------------------------------------------------------------</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>The regional effect of the recruitment to North West Rough (used as reference fishing ground) on the recruitment to other fishing grounds.</td>
<td>Sandeel area 1: ( \gamma_g &gt; 1 ) at Lisborgs Revle ( (P=0.0012) ). Remaining fishing grounds had ( 0 &lt; \gamma_g &lt; 1 ) ( (P&lt;0.0001 ) in both cases).</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>The regional effect of population abundance of age 1 fish on the catch rates of age 1 fish on the individual fishing grounds.</td>
<td>( \eta_g ) was significantly different from zero ( (P&lt;0.0001) ) but not significantly different from 1 ( (P=0.0718) ).</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Dependence of local recruitment in year ( y ) on local recruitment in the previous year to the same fishing ground.</td>
<td>No significant effect of local recruitment the previous year ( (P=0.1170, \kappa = 0) ).</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Dependence of local mortality on local cohort density.</td>
<td>N. W. Rough and Southernmost Rough: ( \beta ) significantly greater than zero ( (\beta=0.21, P=0.0218) ), indicating that mortality increased with increasing density. Shetland: ( \beta ) significantly greater than zero ( (\beta = 0.27, P=0.0003) ), indicating</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
that mortality increased with increasing density.
Fig. 1. Named fishing grounds and numbered sandeel areas referred to in the study.
Fig. 2. Catch rates by fishing ground in area 1 at low, median and high densities at North West Rough. Note difference in scale of the three plots. Fishing grounds are ordered according to increasing distance to North West Rough. Catch rates did not differ significantly between fishing grounds more distant than Rute 18.
Fig. 3. Average catch rate of 1-year olds ('000/min) at 14 fishing grounds as a function of average catch rate at N. W. Rough. Fishing grounds are ordered according to distance to North West Rough, with letters higher in the alphabet indicating more distant fishing grounds: In assessment area 1 (black diamonds), Lisborgs Revle (a), Stenkanten (b), Rute 18 (c), Southernmost Rough (d), S.W. Patch (e), Sorel (f), Outer Well Bank (g), Elbow Spit (h), Tail End (i). In assessment areas 4 (grey diamonds), Eventyr Banke (j), Berwick Bank (k), Marr Bank (l), Wee Bankie (m), and in 2 (open diamonds), N. of Horn (n) and Pigekammeret (o). All fishing grounds in assessment area 1 plotted in one panel are also shown (p). Each symbol represents one year, bars indicate confidence limits of the mean, broken lines are ground specific regressions.

Fig. 4. Catch rates at all grounds as function of number of 1-year olds according to the ICES assessment in area 1 (10⁹). Hatched line shows the predicted average catch rate.
Fig. 5. Average log catch rate (catch in numbers per minute) in the current year of 2-year olds as a function of average log catch rate of 1-year olds the preceding year. N. W. Rough (a), Southernmost Rough (b) and all fishing grounds with at least 5 years of data (c). Horizontal lines represent 95% confidence limits of the mean, lines are ground specific average predictions.
Fig. 6. Average $-k = \ln \hat{C}_{1,y-1} - \ln \hat{C}_{2,y}$, an indicator of total mortality combined with relative catchability of ages 2 and 1.
Fig. 7. Index of abundance of sandeel of age \( a \) in year \( y \) as a function of the abundance of 1-year younger fish the previous year. Diamonds: 1-year olds, squares: 2-year olds, triangles: 3 year olds and circles: 4 year olds. Hatched line indicates a slope of 1, solid line is a regression line common for all ages assuming gamma error distribution of \( C_{a,y} \). Data from sandeel at Shetland by Cook (2004).
Fig. 8. The combined effect of local density dependent recruitment and mortality. Index of total mortality as a function of an index of total abundance of sandeel in area 1. Left panel: estimated for all fishing grounds. Right panel: estimated for all fishing grounds except S. W. Patch. Light grey dotted line: density dependent recruitment and density independent local mortality. Dark grey broken line: density independent recruitment and density dependent local mortality. Black solid line: density dependent recruitment and density dependent local mortality. Vertical lines at the axis indicate annually observed abundance indices. Lines are scaled to be 1 at the median abundance index.
Fig. S1. Residual plots for reduced model 1 (\(\ln \bar{C}_{1,g,y} = k_g + \gamma_g \ln \bar{C}_{1,NWrough,y} + \omega_{g,y} + \varphi_v\)) for grounds in assessment area 1.
Fig. S2. Residual plots for reduced model 2 ($\ln \hat{C}_{1,g,y} = k_g + \eta_g \ln R_{1,y} + \omega_{y,g} + \varphi_v$) for grounds in assessment area 1.
Fig. S3. Residual plots for reduced model 4 ($\ln\tilde{C}_{2,y+1} = k_0 + k_1y + (1 - \beta)\ln\tilde{C}_{1,y} + g_y + \varphi_y$) for N. W. Rough and Southernmost Rough.
Temperature and body size affect recruitment and survival of sandeel across the North Sea

Henriksen, O., Rindorf, A., Brooks, M. E., Lindegren, M., & van Deurs, M.

*Draft manuscript in preparation*
Title: Temperature and body size affect recruitment and survival of sandeel across the North Sea

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Keywords: Short-lived species, forage fish, climate change, recruitment, productivity, length, Ammodytes, ontogeny

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

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

Lesser sandeel (also Raitt’s sandeel, Ammodytes marinus) is one of the most abundant forage fish species in the North Sea and is considered as an essential part of the mid-trophic level in the ecosystem (Furness, 2002). Behaviour, life history, and geographical distribution within the North Sea is thoroughly described in the scientific literature (e.g. Macer, 1966; Winslade, 1974a, 1974b, 1974c; Wright and Bailey, 1996; van Deurs et al., 2010) and research has demonstrated the effect of temperature (e.g. linked to climate change) on productivity and survival of early life stages (i.e. indicated by the recruitment) (e.g. Arnott and Ruxton, 2002; van Deurs et al., 2009; Lindegren et al., 2018). However, the effect of temperature later in life remains largely unresolved. Furthermore, studies that have reported temperature-recruitment correlations are mainly conducted at the regional scale (i.e. the central or western North Sea) using data with little or no spatial resolution.
The life cycle of lesser sandeel (hereafter just "sandeel") includes distinct phases. Sandeel hatch from eggs attached to sand grains and begin a short larval drift phase before developing active swimming and juvenile schooling behavior (Potter and Lough, 1987; Proctor et al., 1998). After metamorphoses at a length of c. 40-50 mm they settle into a patchwork of sandy habitats in the North Sea in early summer, joining the adult segment of the population (Christensen et al., 2007, 2008, 2009). After settling, they immediately adopt adult behavior that includes nocturnal burying and high site fidelity (Wright et al., 2000, 2019; Holland et al., 2005). Maturation occurs around the age of two (Boulcott et al., 2007). The annual cycle of settled juveniles and adults is divided into feeding and overwintering phases. During overwintering, the fish bury in the sand, surviving on energy reserves (van Deurs et al., 2011b). The overwintering extends from late summer, interrupted only by spawning in January (Gauld and Hutcheon, 1990). Juveniles may postpone burying for a couple of months to gain additional resource storage (Reeves, 1994; van Deurs et al., 2010, 2011a). During spring, they emerge again from the sand to forage during the day and bury in the sediment at night (Winslade, 1974; Freeman et al., 2004).

Sandeel productivity in the North Sea is possibly affected by temperature during multiple life-stages. Gonad investment is inhibited at high winter temperatures (Wright et al., 2017a, 2017b) while spawned demersal eggs develop faster (Régnier et al., 2018), resulting in fewer eggs, earlier hatching and smaller sizes of the hatching larvae. The pelagic larvae are assumed to drift passively with the prevailing current (Berntsen et al., 1994; Christensen et al., 2007, 2008) while the temperature of the surrounding water determines growth and survival (Gurkan et al., 2012, 2013). After settlement, temperature may influence growth conditions (Rindorf et al., 2016), which in turn determine the timing of the onset of overwintering. When overwintering...
has begun, bottom temperature determines the rate at which energy reserves are expended (van Deurs et al., 2011b).

In the present study, we examined which phases of the sandeel life cycle population dynamics are influenced by changes in temperature. We used statistical models to test a sequence of temperature hypotheses (Fig. 1 and Table 1) with age-structured abundance indices calculated for nine distinct subareas (Fig. 2A). In the models, population dynamics were expressed as either recruitment (abundance index of age-0 fish) or abundance of young adults (abundance index of age-1). Since density dependence and body size have been proposed as major drivers of population dynamics, these factors were included in the models together with temperature (van Deurs et al., 2009; Eliasen et al., 2011; Lindegren et al., 2018). Abundance indices were derived from a scientific sandeel survey that has been running in early winter (November-December) every year since 2004, covering most of the North Sea (ICES, 2016). While the International Council for the Exploration of the Seas (ICES) uses the survey for stock assessments, it is used here for the first time in a research context.

**Materials and methods**

**Survey data**

Denmark initiated a survey program in 2004 in order to estimate recruitment for the ICES sandeel stock assessments. The survey uses a modified scallop dredge to measure the abundance of sandeel in the seabed during nighttime in late November or early December. The survey covers most of the sandeel habitat in the North Sea and uses a fixed station design, even though the surveyed area has gradually expanded over time and therefore new stations have
been added. At each fixed survey station, three 10 minute hauls are conducted in a way so that each haul intercepts the position about half way and with an angle to the other hauls (i.e. ideally the three hauls form a star). Samples are weighed and all fish are counted and measured (total length rounded down to the nearest half-centimeter). Ten sandeel from each half-centimeter length-class (or all if fewer than 10 are available) are weighed (in grams with two decimals), and aged based on the number of otolith winter-rings. In case of very large catches, a sub-sample is weighed and counted and total number of sandeel is estimated by scaling up to the weight of the total sample.

Abundance indices

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

**Growth indices**

Growth was analyzed by using two indicators, length and condition factor, reflecting long-term and medium-term balance between feeding and metabolism, respectively. Length at age (cm) was calculated by year and subarea using the ALKs mentioned in the section above. Weight at age (g) was calculated based on a length-weight relationship (power function) fitted to the observed lengths and weights for each combination of age, year, and subarea. Condition factor at a given age was estimated as \( C = \frac{W}{L^b} \), where \( W \) is the weight at age, \( L \) is the length at age, and \( b = 3.06 \) (adopted from van Deurs *et al.*, 2013).

**Temperature indices**

Estimates of sea bottom temperature (SBT) and sea surface temperature (SST) for all years (2003-2018) were obtained from the North-West European Shelf – Ocean Physics Reanalysis from MetOffice issued under the European Commission (Copernicus website: [http://marine.copernicus.eu/](http://marine.copernicus.eu/)). The dataset offers daily temperature estimates across a grid consisting of longitudinal-latitudinal 7 km² cells. To achieve subarea-specific estimates of SBT and SST, temperature estimates were averaged across grid cells overlapping the geographical extent of the subareas (Figure 2A). Besides the spatial dimension of temperature, the temporal dimension were also considered by averaging across critical time windows, following recommendations from van de Pol *et al.* (2016). In total, ten different average temperatures (SBT or SST), covering eight different life phases, were calculated. The supposition was that one or more of the first five temperatures influence the abundance of age-0 sandeel, whereas,
one or more of the remaining five temperatures influence the abundance of age-1 sandeel (Table 1 and Fig. 1).

**Effects of temperature, population size and growth**

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

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

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

\[ T_{p,i,y} + I_{1,i,y} + I_{1,i,y-1} + L_{0,i,y} + C_{0,i,y} \]

\[ T_{p,i,y} + I_{0,i,y-1} + L_{1,i,y} + C_{1,i,y} \]

where \( I_{a,i,y} \) is the logarithm-transformed (ln) abundance index for a given age \( (a) \), subarea \( (i) \), and year \( (y) \), \( T_{p,i,y} \) is the average temperature during a given life phase \( (p) \), subarea, and year, \( L_{a,i,y} \) and \( C_{a,i,y} \) are the average length and condition factor at a given age, subarea, and year. Random effects of subarea and year on the intercept were included in both models. However, since the year effect was assumed not be constant across all nine subareas, the random year effect was modeled as an interaction term with management area (see management areas in Fig. 2A). Since five different temperature hypotheses were tested for each age group, each of the models described above were fitted five times, each time using a different temperature (see Table 1 and Fig. 1).

Model selection was performed by comparing all models using \( \text{AIC}_c \) (Hurvich and Tsai, 1989, 1995). If competing models obtained similar scores, i.e. \( \Delta \text{AIC}_c < 2 \) (Burnham and Anderson 1998), then the simplest model with only significant predictors \( (p < 0.05, \text{Wald } Z\text{-statistics}) \) was chosen as the final model. However, even if temperature was not part of the simplest
model, it was re-introduced to the final model to obtain information about the slope estimate.

To investigate if local differences in the response to temperature existed between subareas, the final model was re-fitted to data from each subarea one by one (leaving out the random effect of subarea).

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

Results

Abundance indices

In all nine subareas, abundance indices fluctuated by a factor of c. 10 (i.e. the actual abundance index and not the logarithm-transformed) between years and no strong temporal trends occurred in any of the subareas (Fig. 2). Year-to-year dynamics differed notably between subareas, except for age-0 abundance in 2009 and 2016, which was above average in all subareas. The internal consistency (i.e. the logarithm-transformed age-1 index in the current year as a function of the logarithm-transformed age-0 index in the preceding year) varied between 15% and 65% explained variance (>40% in five out of nine subareas) (see supplementary material, Fig. S1).

Effects of temperature, population size and growth

After model reduction, the final model for age-0 abundance included the positive effect of fish length as the only significant predictor ($p < 0.004$, Wald Z-statistics) (see supplementary
material, Table S1, Fig. S2, Fig. S3 for more details about model selection and model fits). The variance explained by fixed effects and combined fixed and random effects was 8% and 72%, respectively (Table 2). The relationship between age-0 abundance and fish length were positive in eight subareas and significant (p < 0.05) in four out of nine subareas (see supplementary material, Fig. S4). No significant correlation between abundance and any of the tested temperature indices was seen in any subarea (see supplementary material, Fig. S5).

After model reduction, the final model of age-1 abundance retained recruitment in the preceding year (i.e. \( I_0 \)) (p < 0.000) and bottom temperature in late summer and autumn (i.e. \( T_8 \)), the first part of the overwintering period (p < 0.003) (see supplementary material, Table S1, Fig. S3, and Fig. S6 for more details about model selection and model fits). The effect of temperature was negative and the effect of recruitment in the preceding year was positive (Fig. 3). The fixed effects explained 44% of the variance and the combined fixed and random effects explained 84% (Table 2).

**Geographical differences in the effect of temperature**

Fitting the final best model formulation to each subarea, showed that the abundance of age-1 sandeel was positively related to recruitment in the preceding year (i.e. positive slope coefficients) in all nine subareas (significant slopes in five subareas) and negatively affected by temperature (\( T_8 \)) in eight out of nine subareas (significantly negative slope in four subareas) (Table 3, Fig. 4A, and Fig. 4B). When the subarea-specific slopes of the temperature effects (from subareas with at least seven years of survey data, see Fig. 2B) were related to the average temperature of the respective subareas (averaged across all years), a highly significant negative relationship appeared (p < 0.001, explained variance = 87%) (Fig. 4D). Geographically, the North Sea could roughly be divided into a northerly offshore cold area consisting of subareas
exposed to average temperatures < 10.5 °C and a southerly and coastal area, consisting of subareas exposed to average temperatures >10.5 °C (Fig. 4C). The estimated slope coefficients were in general more negative (i.e. stronger temperature effect) in the warmer area (Fig. 4A).

Since none of the temperatures (\(T_1\) to \(T_5\)) contributed significantly to the age-0 model, the results obtained from fitting the model to each subarea, is only presented in the supplementary material (see supplementary material, Table S2).

**Discussion**

The influence of temperature on sandeel abundance differed between the first year of life and second year of life. During the first year of life, no relationship with temperature was found for any of the five temperatures tested. In contrast, during the second year of life, the change in abundance of age-0 was significantly related to bottom temperature at the beginning of the overwintering period (\(T_8\)), and southerly areas experiencing higher average temperatures responded more strongly to variation in temperature than northern areas with lower average temperatures.

In line with the findings here for age-0 sandeel, previous studies that have used either recruitment numbers from stock assessment models or indices of recruitment (i.e. larvae abundance) have failed to establish robust relationships with temperature (Lynam et al., 2013; Carroll et al., 2017; Eerkes-Medrano et al., 2017). In contrast, studies using recruitment per spawner biomass, based on output from stock assessment models, have found negative relationships with temperature (Arnott and Ruxton, 2002; Lindegren et al., 2018). This
inconsistency could potentially be attributed to the inclusion of spawning stock biomass when calculating recruitment per spawner, which emphasizes a relatively distinct underlying stock-recruitment relationship. Assuming such a relationship, as in a Ricker model, has been debated on several occasions in relation to short-lived species (Vert-Pre et al., 2013; Szuwalski et al., 2015). Hence, in the present study we chose not to force the model by making assumptions regarding the stock-recruitment relationship. The above mentioned inconsistency, could, however, also be attributed to differences in time-series lengths, the data sources, the spatial resolution of the data, or the model approaches.

Higher bottom temperature during the beginning of the overwintering period, significantly decreased abundance of age-1 sandeel across the North Sea. Energy budget modelling has suggested that starvation and/or predation, not temperature, are the two main factors driving survival of older sandeel (MacDonald et al., 2018). No direct effect of temperature on survival of age-1 overwintering sandeel has been confirmed (MacDonald et al., 2019). The experimental studies to date, have not investigated the lethal effects accounting for food limitation and predation. Nevertheless, these studies did find that temperature had a negative effect on individual mass change during overwintering (Wright et al., 2017b, 2017a), which supports notions about increased energetic cost of overwintering (van Deurs et al., 2011b). The predation pressure on sandeel from other fish species is high (Heath et al., 2009). Several authors have noted that the removal of sandeel by predatory fish greatly exceeded that of the fisheries, seabirds, and marine mammals combined (Engelhard et al., 2014). Furthermore, so-called “aggregative responses” by whiting and haddock have been shown to greatly impact local sandeel biomasses (Temming et al., 2004, 2007). If high water temperatures in fall and winter force the sandeel to reduce the duration of the overwintering period for reasons related to bioenergetics (van Deurs et al., 2010, 2011b), this may increase predation mortality and
reduce abundance. In addition, as a consequence of ocean warming, several marine species interacting with sandeel (via predation or competition), have either increased in abundance in the North Sea or expanded their distributions into the North Sea (Attrill et al., 2007; ter Hoïstede et al., 2010; Petitgas et al., 2012; Cormon et al., 2016). Further, their food intake may increase with temperature if food processing time is a limiting factor (Reilly et al., 2014).

The effect of fish length on abundance of age-0 sandeel was highly significant. This is in agreement with the classical “Stage-Duration” hypothesis (Anderson, 1988), implying that “bigger is better” and fast growth improves survival early in life (Miller et al., 1988). Bigger is also better for avoiding starvation, since mass-specific metabolism during overwintering decrease with increasing size (van Deurs et al., 2011b). Thus, confirming that the main factors affecting survival of sandeel during the first year of life are changes in food condition and predation mortality (Eliasen et al., 2011; MacDonald et al., 2018, 2019). Different mortality pathways have been proposed for first-feeding larvae (Wright and Bailey, 1996; Henriksen et al., 2018), the larval drift phase (Gurkan et al., 2012, 2013), and overwintering of post-settled juveniles (van Deurs et al., 2011b; MacDonald et al., 2018). A potential close relationship with Calanus copepods has been investigated on several occasions (van Deurs et al., 2009, 2014, 2015; Régnier et al., 2017). However, other studies have argued that drivers, such as the physical oceanography, dictate the conditions for growth and survival during the larval phase, including successful retention near suitable habitats (Gurkan et al., 2013; Henriksen et al., 2018). Alternative explanations for the strong relationship with length could be length-dependent catchability in the survey or correlations between recruitment, length and a third factor such as temperature. The former was tested for in a previous study and was not found to be a problem (Johnsen and Harbitz, 2013). Regarding the effect of temperature on fish length,
this was only found to be significant in one out of nine subareas (Fig. S7), indicating that the length effect is not driven by an underlying indirect temperature effect.

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

The effect of temperature was strongest in the southern half of the North Sea. The North Sea can, in terms of temperature, be divided into a northernly cold region and a southerly/coastal warmer region (see Fig 5). The latter are shallow and also largely devoid of thermoclines (Luyten et al., 2003). These features make the area particularly susceptible to ocean warming, and as a result, the North Sea demersal fish assemblages are responding by moving to deeper waters (Dulvy et al., 2008). Hence, the impacts are expected to increase in future years, possibly to the point where stationary stable sandeel populations will no longer be viable in southern areas. In contrast, the northeastern sandeel habitats are situated in deeper waters (Rindorf et al., 2016), where thermoclines offer colder bottom temperatures throughout the year, making these areas possibly more resilient to future warming oceans.

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

Acknowledgements:

The project was funded by the European Fisheries and Maritime Fund and Ministry of Environment and Food in Denmark (33113-B-16-080). We also want to thank the many people that have contributed over time to uphold the Danish sandeel survey and the laboratory personal that have counted, measured, and aged the fish.

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Table 1. Detailed summary of the different temperature hypotheses.

<table>
<thead>
<tr>
<th>Age group of concern</th>
<th>Description of link between temperature and life phase</th>
<th>Expected effect direction</th>
<th>Temperature abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>SBT experienced by parents prior to spawning</td>
<td>Negative</td>
<td>T₁</td>
</tr>
<tr>
<td>0</td>
<td>SBT during egg incubation and hatching</td>
<td>Positive/Negative</td>
<td>T₂</td>
</tr>
<tr>
<td>0</td>
<td>SST during the larval drifting phase</td>
<td>Positive</td>
<td>T₃</td>
</tr>
<tr>
<td>0</td>
<td>SST during the post-settlement foraging</td>
<td>Positive</td>
<td>T₄</td>
</tr>
<tr>
<td>0</td>
<td>SBT during the first months of juvenile overwintering until the sandeel survey takes place</td>
<td>Negative</td>
<td>T₅</td>
</tr>
<tr>
<td>1</td>
<td>SBT during the full overwintering period</td>
<td>Negative</td>
<td>T₆</td>
</tr>
<tr>
<td>1</td>
<td>SBT during the second half of the overwintering period</td>
<td>Negative</td>
<td>T₆ₐ</td>
</tr>
<tr>
<td>1</td>
<td>SBT during the second half of the overwintering period</td>
<td>Negative</td>
<td>T₆₉</td>
</tr>
<tr>
<td>1</td>
<td>SST during the annual foraging window starting in spring</td>
<td>Negative</td>
<td>T₇</td>
</tr>
<tr>
<td>1</td>
<td>SBT during the first months of the adult overwintering period until the sandeel survey takes place</td>
<td>Negative</td>
<td>T₈</td>
</tr>
</tbody>
</table>
Table 2. Summary statistics from the final mixed effects models for age-0 and age-1 after model selection. The dependent variables were logarithm-transformed (ln) abundance indices for age-0 \( (I_0) \) and age-1\( (I_1) \). The best age-0 model included only fish length \( (L) \). The best age-1 model included temperature during the early overwintering period \( (T_8) \) and recruitment in the preceding year \( (I_{0,y-1}) \). Numbers in parentheses are SE for estimates of fixed effect coefficients and SD for random effects. Also, the variance explained for fixed effects \( (R^2_m) \), combined fixed and random effects \( (R^2_c) \), and the p-values (*p < 0.05, **p < 0.01, ***p < 0.001, Wald Z-statistics) are presented.

<table>
<thead>
<tr>
<th>Model</th>
<th>Final model</th>
<th>( R^2_m / R^2_c )</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age-0</td>
<td>( I_{0,i,y} \sim L_{0,i,y} )</td>
<td>0.08/0.72</td>
<td>101</td>
</tr>
<tr>
<td>Age-1</td>
<td>( I_{1,i,y} \sim T_{8,i,y} + I_{0,i,y-1} )</td>
<td>0.44/0.84</td>
<td>81</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>p-value</th>
<th>StdDev</th>
<th>Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age-0 Length</td>
<td>(0.140)</td>
<td>0.004**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Random Effect of Subarea</td>
<td>0.988</td>
<td>9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age-1 Temperature</td>
<td>(0.144)</td>
<td>0.003**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Recruitment</td>
<td>(0.086)</td>
<td>0.000***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Random Effect of Subarea</td>
<td>0.825</td>
<td>9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
### Table 3. Summary statistics from mixed effects models fitted to data from each of the nine subareas (n designates the length of the survey time-series of each subarea). Fixed effects were based on the final best age-1 model, which included temperature ($T_8$) and recruitment of age-0 fish in the preceding year ($I_{0,y-1}$). The variance explained for fixed effects ($R^2_m$), combined fixed and random effects of year ($R^2_c$), slope coefficients, and p-values (*p < 0.05, **p < 0.01, ***p < 0.001, Wald Z-statistics) are presented. Numbers in parentheses are SE for estimated fixed effect slopes.

<table>
<thead>
<tr>
<th>Subarea</th>
<th>n</th>
<th>$R^2_m$/$R^2_c$ Slope($T$)</th>
<th>p($T$)</th>
<th>Slope($I_{0,y-1}$)</th>
<th>p($I_{0,y-1}$)</th>
<th>StdDev estimates</th>
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<tbody>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Random effect of year</td>
</tr>
<tr>
<td>1</td>
<td>14</td>
<td>0.45/0.63</td>
<td>-0.729</td>
<td>0.049*</td>
<td>0.444</td>
<td>0.049*</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.370)</td>
<td>(0.226)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>0.27/0.51</td>
<td>-0.623</td>
<td>0.339</td>
<td>0.163</td>
<td>0.679</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.651)</td>
<td>(0.396)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>8</td>
<td>0.54/0.56</td>
<td>-0.336</td>
<td>0.322</td>
<td>0.522</td>
<td>0.009**</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.339)</td>
<td>(0.202)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>5</td>
<td>0.18/0.33</td>
<td>-0.379</td>
<td>0.704</td>
<td>0.309</td>
<td>0.356</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>(0.998)</td>
<td>(0.335)</td>
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<tr>
<td>5</td>
<td>13</td>
<td>0.64/0.70</td>
<td>-0.456</td>
<td>0.086</td>
<td>0.534</td>
<td>0.000***</td>
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<tr>
<td>6</td>
<td>10</td>
<td>0.51/0.59</td>
<td>-0.801</td>
<td>0.019*</td>
<td>0.522</td>
<td>0.052</td>
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<tr>
<td>7</td>
<td>12</td>
<td>0.38/0.59</td>
<td>-0.966</td>
<td>0.024*</td>
<td>0.411</td>
<td>0.147</td>
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<tr>
<td>8</td>
<td>7</td>
<td>0.73/0.80</td>
<td>-0.801</td>
<td>0.009**</td>
<td>0.869</td>
<td>0.005**</td>
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</tr>
<tr>
<td>9</td>
<td>4</td>
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<td>0.332</td>
<td>0.569</td>
<td>0.867</td>
<td>0.000***</td>
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</table>
Figure 1. Schematics of hypotheses of how different temperatures relate to different phases of the sandeel life cycle. (a) five different phases during the first year of life (age-0) illustrated by pictograms connected by arrows, starting with mature sandeel prior to spawning (i.e. egg developing in gonads), then the egg phase, larval phase, and metamorphosis, and finally ending with the first half of the first overwintering period. Temperature hypotheses are illustrated by black boxes (T₁ to T₅). (b) Three phases of the second year of life (age-1) illustrated by
pictograms connected by arrows, starting with the second half of the first overwintering period, followed by a feeding period, and ending with the first half of the second overwintering period. Temperature hypotheses are illustrated by white boxes (T_6 to T_8). (c) Illustration of how each temperature hypothesis (reusing the boxes in panels a and b) uses an average temperature, covering four or more months. Months are illustrated by arrow-boxes with the first letter of each month inside. The extent and position of horizontal lines shows which months is used for the respective average temperatures. Sea surface temperature is represented by dashed lines and bottom temperature by solid lines. The timing of the Danish sandeel survey are illustrated by ship-pictograms.
Figure 2. (A) Map of sandeel habitat (polygons) and survey stations (black dots). The color-coding of the polygons represent the nine subareas used in the study. Sandeel habitat not used in the present study are shown in grey shading. ICES sandeel management areas SA1, SA2, and SA3 are superimposed on top of the subareas. (B) Time-series of log transformed abundance indices produced from survey data for age-0 (solid lines) and age-1 (dashed lines), respectively. Differences in time-series lengths are due to the survey being expanded (geographically) in 2006, 2011, and 2014. Missing years are due to insufficient data to produce reliable age-length-keys (See description in Materials and Methods).
Figure 3. Observed (points) and model predicted (lines) of sandeel abundance (age-1). (A) Relationship between ln(age-1 index) and temperature during the early part of the overwintering period ($T_8$). Predictions are shown for low (red; below 1$^{\text{st}}$ quartile), medium (green; between 1$^{\text{st}}$ and 3$^{\text{rd}}$ quartile), and high (blue; above 3$^{\text{rd}}$ quartile) recruitment, respectively. (B) Relationship between ln(age-1 index) and ln(age-0 index) in the preceding year (i.e. proxy for previous year’s recruitment). Predictions are shown for low (red), medium (green), and high (blue) $T_8$, respectively.
Figure 4. Maps showing spatial variation in average temperature, slopes, and p-values (A-C). Relationship between slope coefficients and the average temperature (D). Each point in the D-panel represents a subarea. Subareas with fewer than seven years of data are indicated by open dots. The regression line was fitted to subareas with at least seven years of data (solid dots). The temperature used in panel-C and panel-D is $T_s$ averaged across all years. ICES management areas are indicated by the shape of the symbols in Panel-D and depicted in panel-B.
Online Supplementary Materials

Survey Index

Abundance indices for age-0 and age-1 were calculated from haul based numbers-at-age from the Danish dredge survey and following the approach used by ICES. Numbers-at-age were calculated using the observed numbers-at-length from standardized 10-minute hauls and estimated age-length-keys (ALKs). The ALKs were assumed constant within years and subareas, and estimated using the methodology from Berg and Kristensen (2012). This method estimates' smooth 'ALKs and provides an objective 'fill-in 'procedure for missing length groups. Abundance indices by age and subarea were then calculated using the previous published alternative method for calculating survey based relative abundance indices (Berg et al. 2014). This method uses a delta-lognormal model which combines a binomial presence/absence model and a lognormal model for strictly positive numbers. In this study, both parts of the delta-lognormal model contained year and subarea as categorical fixed effects and a random intercept of year interacting with subarea. Separate sets of model parameters were estimated for each age group. The model is used to predict abundances on a grid of points that is the same for all years. When having estimated grid-point abundances, the survey index for the desired area is simply calculated by summing up the abundances of grid-points contained within the desired area.
To scale the final abundance index of a given age to the surface area of each subarea, a $1 \times 1$ km grid was overlaid the sandeel habitat polygons that make up the nine subareas (see Fig. 2A in the main text). The model was then used to predict abundances within each grid cell. Lastly, the final abundance index was obtained by summing up all grid cells within each subarea. The main differences between the indices of abundance calculated in the present study and those reported by ICES for the sandeel stock assessment models were: (i) ICES sums up grid cells within each assessment area and not just within each subarea, and (ii) ALKs in the present study were estimated by subarea, whereas ICES uses stock assessment area (Fig. 2A in the main text shows both the subareas and the assessment areas). For more details please see ICES (2016) and Berg et al. (2014).


Additional tables and figures containing supporting information

The following tables and figures contain supporting information. For example, an additional level of details, which is not necessary for understanding the analyses and conclusions described in the main text, but which may still be of interest to some readers. The main text refers to each of the tables and figures below, where appropriate, as supplementary (S) information (i.e. Table S1 or Fig. S1).

Table S1 Summary statistics for model selection of candidate models (i.e. Age-0 and Age-1) for different periods of temperatures ($T$). P-values for all covariate slopes are also indicated in parentheses *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

<table>
<thead>
<tr>
<th>$T$</th>
<th>Age</th>
<th>n</th>
<th>AICc</th>
<th>DF RE</th>
<th>DF residual</th>
<th>$R^2_m$ / $R^2_c$</th>
<th>T</th>
<th>L</th>
<th>I₀</th>
<th>I₁</th>
<th>Final model</th>
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<tr>
<td>Age-0: $I_{0,y} \sim T_y + I_{1,y} + C_{0,y} + L_{0,y}$</td>
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<td>T₁</td>
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<td>101</td>
<td>333.31</td>
<td>9</td>
<td>38</td>
<td>0.08/0.72</td>
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<td>$I_{0,y} \sim L_{0,y}$</td>
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<td>9</td>
<td>38</td>
<td>0.08/0.72</td>
<td>-</td>
<td>0.398</td>
<td>NA</td>
<td>-</td>
<td>$I_{0,y} \sim L_{0,y}$</td>
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<td>(0.140)</td>
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<tr>
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<td>0</td>
<td>101</td>
<td>333.31</td>
<td>9</td>
<td>38</td>
<td>0.08/0.72</td>
<td>-</td>
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<td>$I_{0,y} \sim L_{0,y}$</td>
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<td>101</td>
<td>333.31</td>
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<td>38</td>
<td>0.08/0.72</td>
<td>-</td>
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<td>-</td>
<td>$I_{0,y} \sim L_{0,y}$</td>
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<td>(0.140)</td>
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<tr>
<td>T₅</td>
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<td>0.08/0.72</td>
<td>-</td>
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<td>-</td>
<td>$I_{0,y} \sim L_{0,y}$</td>
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<td></td>
<td>(0.140)</td>
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<tr>
<td>Age-1: $I_{1,y} \sim T_y + I_{0,y} + I_{1,y} + C_{1,y} + L_{1,y}$</td>
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Table S2. Summary statistics from mixed effects models (of age-0 abundance) fitted to data from each of the nine subareas, separately. The models were a slight modification of the final best age-0 model (see materials and methods) and included temperature ($T_x$) and length in the preceding year ($L$). The variance explained for fixed effects ($R^2_m$) and combined fixed and random effects of year ($R^2_c$), slope coefficients, and p-values (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) are presented. Numbers in parentheses are SE for estimated fixed effect slopes.

<table>
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<tr>
<th>Subarea</th>
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<th>$R^2_m$/$R^2_c$</th>
<th>Fixed effects</th>
<th>StdDev estimates</th>
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<td>Slope($T$)</td>
<td>p($T$)</td>
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<td>0.15/0.57</td>
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<tr>
<td>2</td>
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<td>0.32/0.62</td>
<td>0.290 (0.472)</td>
<td>0.538</td>
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<tr>
<td>3</td>
<td>9</td>
<td>0.13/0.40</td>
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<td>---</td>
</tr>
<tr>
<td>4</td>
<td>14</td>
<td>0.98/0.99</td>
<td>1.731 (0.359)</td>
<td>0.000***</td>
</tr>
<tr>
<td>5</td>
<td>14</td>
<td>0.45/0.61</td>
<td>1.557 (0.610)</td>
<td>0.011*</td>
</tr>
<tr>
<td>6</td>
<td>9</td>
<td>0.19/0.32</td>
<td>0.434 (0.617)</td>
<td>0.481</td>
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<tr>
<td>7</td>
<td>14</td>
<td>0.64/0.78</td>
<td>0.034 (0.451)</td>
<td>0.939</td>
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<tr>
<td>8</td>
<td>14</td>
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<td>1.249 (0.685)</td>
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<tr>
<td>9</td>
<td>7</td>
<td>0.26/0.50</td>
<td>-0.870 (1.246)</td>
<td>0.485</td>
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</table>

**Figure S1.** Logarithm-transformed age-1 abundance index in the current year as a function of the Logarithm-transformed age-0 index in the preceding year (also known as internal consistency), shown for all nine subareas (in reading direction) (color code matches map in [Image])
figure 2A). Explained variance ($R^2$) and statistics for Pearson correlation test is shown for each subarea.

Figure S2. Model diagnostics of best final model for age-0
Figure S3. ΔAIC (A) and estimates of slope coefficients (B) for temperature in ten models. Ten different temperatures representing ten different ontogenetic stages where added, one by one, to the final best model (represented at ΔAIC = 0, dashed line) of age-0 (dots) and age-1 abundances (triangles), respectively. The final best age-1 model already included temperature in the early stages of the overwintering period (T3), hence, this temperature was replaced by the remaining temperatures, one at the time. SE of the slope estimates are illustrated by vertical whiskers.
Figure S4. The relationship between abundances of age-0 sandeel and length for all subareas 1 to 9 (color code matches map in Fig. 2A). Explained variance ($R^2$) and statistics for Pearson correlation test is shown for each subarea.
Figure S5. The relationship between abundances of Age-0 sandeel and annual SST for all subareas 1 to 9 (color code matches map in Fig. 2A). Explained variance ($R^2$) and statistics for Pearson correlation test is shown for each subarea.
Figure S6. Model diagnostics of best final for age-1

Figure S7. Relationships between length of age-0 sandeel and annual sea surface temperature (SST) for subareas 1 to 9 (color code matches map in Fig. 2A). Explained variance ($R^2$) and statistics for Pearson correlation test is shown for each subarea. Note that the number of data points varies between subareas, which is because length-data were not available for all combinations of year and subarea.
Get up early: climate change leads to behavioral changes in sandeel.

Henriksen, O., Rindorf, A., Payne, M., Mosegaard, H., & van Deurs, M.

Draft manuscript in preparation
Get up early: climate change may lead to behavioral changes in sandeel

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Abstract: Warming of the oceans is likely to cause site-attached species to change behavior or experience changes in productivity. The present study explores the role of temperature on the overwintering behavior of the North Sea lesser sandeel (Ammodytes marinus). In spring, sandeel emerge from their overwintering refuge in the sandy bottom to feed and grow. Using fisheries data from four areas in the North Sea, we developed indicators of the relative timing of emergence. Year-to-year variation in these proxies were found to be correlated to variation in temperature. Colder years were characterized by delayed emergence and vice versa. The causal mechanisms involved were investigated through a series of simple linear regression models and a bioenergetics model. Both temperature by itself and when used to force the bioenergetics model (together with fish length), revealed significant relationships with temperature. However, also fish length by itself correlated to timing of emergence. Hence, although the support for the different hypotheses were somewhat inconclusive, the main part of the results leans towards an explanation related to bioenergetics. The study emphasizes some of the behavioral changes of sandeel that is likely to occur as a response to the gradual warming of the North Sea caused by climate change.
Introduction

Temperature is an essential driver of a variety of ecosystem dynamics (Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2006) and the general expectations is that warming of the oceans in the temperate and arctic hemisphere will dampen seasonality and shift the timing of transitions between seasons (Burrows et al., 2011). Species showing high degree of site fidelity, such as sandeel (Ammodytidae), are likely to be more sensitive to increasing temperatures and shifts in the transition between seasons as their ability to mitigate climate effects by moving are limited (Heath et al., 2012; Pecl et al., 2014).

Lesser sandeel Ammodytes marinus (hereafter just referred to as sandeel) endure winter periods of low food availability by storing energy reserves during a feeding season (mainly spring) for use in the subsequent burying phase, where they survive solely on these reserves (van Deurs et al., 2010, 2011). The burying phase lasts for up to nine months, sometimes starting as early as late summer (hereafter referred to as the overwintering period even though it covers more than just the winter months). Towards the end of the overwintering period, they will gradually emerge from the sand, with the youngest appearing first, to feed in shoals during the day (retreating to the sand each night). The suitability of this strategy relies on the delicate balance between food intake in a short feeding period and the expenditure during the extended overwintering period. The timing and duration of the overwintering period (incl. the timing of emergence in spring) have previously been linked to temperature and food availability (Winslade, 1974a, 1974b; van Deurs et al., 2010, 2011), indicating that increasing temperatures or shifts in the primary and secondary production can shift this balance, forcing the sandeel to emerge from their overwintering state earlier and stay in the feeding phase longer. As sandeel are most vulnerable to predators when leaving and entering sediments (Hobson, 1986; Temming et al., 2004, 2007; Johnsen et al., 2017), such changes may lead to increased predation mortality. Furthermore, since sandeel in the North Sea play a major role in the diet of predatory fish, seabirds, and mammals in spring and summer, shifts in the timing of emergence is likely to have ecosystem wide effects (Harris and Wanless, 1991; Greenstreet et al., 1998; Furness, 2002; Sharples et al., 2009; de Boer, 2010; Engelhard et al., 2014; Gilles et al., 2016).
A hindrance to the coupling of climatic variation and timing of shifts between season-
determined behavioral strategies in wild fish, is the need for long biological time-series (i.e.
decades), which at the same time covers multiple months of years (Brown et al., 2011; Bates
et al., 2014). However, commercial catch data often fulfill these requirements. Sandeel in the
North Sea is a major component of the industrial fishery and is used for fishmeal and fish oil
(Nielsen, 1989; Furness, 2002; Nielsen and Mathiesen, 2006; Dickey-Collas et al., 2014). The
catches of this highly seasonal sandeel fishery follows roughly a dome-shaped curve from
March/April until June/July and with a peak around May (Reeves, 1994) (see also schematics
in Fig. 1). It has been hypothesized that the increase in catch rates in spring reflects a
combination of emergence from winter dormancy in the sand and rapid growth (van Deurs et
al., 2013; Rindorf et al., 2016; Johnsen et al., 2017). The subsequent decline is presumably
when feeding activity starts to fate, growth stagnates, and the sandeel once again spent more
and more time submerged in the sand (Macer, 1968; Reeves, 1994; Kvist et al., 2001; van
Deurs et al., 2013).

In the present study, we investigated year-to-year variation in the relative timing of emergence
of sandeel using commercial catch rates and related this variation to variation in temperature,
primary production (as an indicator of food abundance), and bioenergetics. We concentrated
on three alternative hypotheses: (Food hypothesis) The increase in food availability in spring
“wakes up” the sandeel. (Trigger hypothesis) Temperature acts as a trigger stimuli “wakening
up” the sandeel. (Bioenergetics hypothesis) Temperature acts indirectly (and in combination
with size) via a bioenergetics pathway, where depletion of energy stores is what “wakes up”
sandeel.

Materials and methods

Catch data

Catches (in tons) and effort (numbers of fishing days) were extracted from individual logbook
records from the Danish industrial fishery (1993-2017) together with information about the
statistical rectangle (those used by the International Council for the Exploration of the Seas
(ICES): 1 longitude × 0.5 latitude). To ensure sufficient spatial and temporal data coverage for
the analysis, only rectangles within four major fishing areas were included: Dogger Bank (DB), Elbow Spit (ES), Fiskebanker (FB) and Horns Rev (HR) (Fig. 2). Today, the fishery is conducted between 1st of April and 1st of August, but in the 1990s a fishery targeting 0-groups took place after 1st of August. 0-group fish arrive at the fishing grounds in late June and remain in the water column long after the older age groups have begun overwintering. To avoid confounding the analysis with data from the 0-group fishery, data after 19th of July (Julian day 200) were excluded. Furthermore, fishing tends to start later in the coastal areas (FB and HR). Hence, for these areas, only data after Julian day 95 (5th of April) and 120 (1st of May), respectively, was included, based on the criteria that at least three logbook records per day should be available.

**Standardization of catch per unit effort**

The average size of vessels has increased substantially throughout the time-series making the catch rates incomparable between areas and years. Further, as the smaller vessels tend to start the season followed by larger vessels, it was necessary to correct the data for differences in vessel size across years and days. This was done by standardising all effort data (number of fishing days) to days equivalent to a 200 GRT vessel using a vessel size correction factor $b$ estimated using the following general formulation of catch per unit effort (CPUE):

$$CPUE_{V,i} = \frac{C_i}{E_{V,i}} = q_0 V^b B$$

, where $C_i$ is the recorded catch in logbook record $i$ and $E_{V,i}$ is the effort of vessel size $V$ (gross tonnage) in logbook record $i$. $q_0$ denotes the catchability of a standard vessel (and is thus independent of changes in size composition in the fleet) and $B$ is biomass. $b$ was estimated through three mixed models having year $y$, ICES statistical rectangle $s$ and week $w$ as mixed effects in four separate periods (1989-1998, 1999-2005, 2006-2016, 2017-2019). The approach assumes that catches within the same rectangle, week, and year are taken at the same biomass $B$. In addition, individual observations of catches by a single vessel were assumed similar to those taken by the same vessel in other areas and times (i.e. $ID$, vessel effect). The specification of each mixed model was as follows:
\ln(CPUE_{w,s,y,ID}) = \varphi_{w,s} + \lambda_{ID} + b \cdot \ln(V)

where \(\varphi_{w,r,s,y}\) and \(\lambda_{ID}\) are separate normal distributed parameters, each with a mean of 0.

Residuals were examined for signs of non-linearity in the relationship between CPUE and \(V\), but no such signs were found. There was a tendency for over-occurrence of large negative residuals in all periods. Standardised effort was estimated as:

\[ E_{200,t} = \left( \frac{V}{200} \right)^b E_{V,t} \]

Hence, as \(b\) is greater than zero, a fishing day of a vessel larger than 200 tonnage will result in a standardised fishing effort of more than one day, whereas a day of fishing on a vessel smaller than 200 tonnage results a standardised fishing effort of less than one day. Catches were unchanged.

**Seasonal patterns in sandeel biomass**

In order to describe the relative differences in the timing of emergence between years, we first had to describe how daytime sandeel biomass in the water column increases after the winter and eventually decreases again as the main feeding period is surpassed. We used CPUE as a proxy for daytime biomass. To overcome the problem of noisy data, we derived the predicted CPUE at any given time, by fitting GAMs to the logarithmically transformed daily CPUE values (restricting the number of knots to 3). Separate GAMs were fitted to each year and area, ideally describing how CPUE increased until a maximum and thereafter decline (Fig. 1). If the fitted curve was only increasing or declining (i.e. reaching either the maximum at the first or the last data-point) \(k\) was increased from 3 to 4. If the problem persisted, the specific year-area combination was excluded from analyses. If a given GAM explained less than 10% of the variance in the CPUE data, the fit was regarded as insufficient and excluded from analyses. Lastly, to ensure that the curvature of the fitted GAMs (i.e. the position of the top point) were sufficiently supported by the data-points, year-area combinations with less than 15 data-points after day 140 (Fig. 3) were excluded from the analyses. GAMs were chosen instead of parametric solutions such as parabolic relationships to avoid the situation where CPUE values
late in the season influence on the increasing part of the relationship. All GAM-fitted curves are shown in the supplementary material (Fig. S1-S4), including indications of which year-area combinations were excluded from the analyses.

**Timing of emergence**

The dates of the initial logbook records in a given year were not a robust indicator of the timing of emergence. Overall fishing effort have decreased since 2003, resulting in a delay of the first logbook record. In addition, the total allowable catch and the start date of the fishery, which is regulated by managers, is also affecting the date of the first logbook record. Hence, quite often, CPUE was already relatively high when the fishing commenced (indicating that first emergence occurred before the first logbook record). Hence, to circumvent this problem, we developed two alternative measures of the relative timing of emergence, using the seasonal peak in CPUE as a reference instead of the first logbook records. The assumption of the first measure was that if predicted CPUE (predicted from the GAM fits) on the first day of fishing ($A_0$) was relatively close to the maximum predicted CPUE ($A_{max}$), the sandeel emerged early, whereas, if $A_0$ was much smaller than $A_{max}$, the sandeel emerged relatively late. Hence, the first measure was calculated as $\Delta A = A_{max} - A_0$. The second measure of the relative timing of emergence used the time difference between the first day of fishing ($D_0$) and the day on which CPUE was close to its maximum. For example, if the time difference is small, emergence happened early and vice versa (provided the first day of fishing is the same every year). A sensitivity test showed that the day where the predicted ln(CPUE) reached 70% of $A_{max}$ (hereafter referred to as $D_{70}$) was better estimated than the day of $A_{max}$ itself (and also better than 60%, 80% and 90%) (Fig. S5). Going below 60% of $A_{max}$ was also not a possibility, since the lowest predicted CPUE was higher than 60% of $A_{max}$ in some years. Hence, the second measure was calculated as $\Delta D = D_{70} - D_0$. $D_0$ was a fixed day (but differed between areas) and defined based on data availability as described in the section above about catch data. Note also that $\Delta D$ is proportional to $D_{70}$ when $D_0$ is a fixed day, but we chose to use $\Delta D$ because $D_{70}$ cannot be smaller than $D_0$. A schematic illustration of $\Delta A$ and $\Delta D$ can be found in figure 1. We will hereafter refer to $\Delta A$ and $\Delta D$ as measures of the timing of emergence, although, these are not estimates of the actual day of emergence, but merely relative proxies designed to describe year-to-year variation. Lastly, we also calculated the slope of the line going through $A_{70}$ and $A_{max}$ as an indication of the rate of increase in ln(CPUE).
**Temperature and phytoplankton**

In order to test for correlations between environmental drivers and timing of emergence, we obtained monthly measures of sea bottom temperature (SBT), sea surface temperature (SST), and mass concentration (mgC m\(^{-3}\)) of phytoplankton (PP) from the MetOffice issued under the European Commission (Copernicus website: [http://marine.copernicus.eu/](http://marine.copernicus.eu/)). Sandeel prey on zooplankton, but in lack of a reliable zooplankton-index, we used PP as an indicator system productivity. The data are the results from the Atlantic-European North-West Shelf-Ocean Physics Reanalysis and, -Biogeochemistry Reanalysis, respectively. Data were downloaded as daily values and in a grid of longitudinal-latitudinal 7 km\(^2\) cells, and from that we calculated monthly averages as well as the minimum winter temperature for all four study areas (Fig. 2). To evaluate the food hypothesis, we correlated timing of emergence to monthly values of PP assuming that significant negative correlations with PP in early spring support the growth hypothesis. To evaluate the trigger hypothesis, we used linear regression analyses to relate timing of emergence to minimum SBT and the day on which the minimum SBT was observed (i.e. the day on which the water begins to warm up), respectively. If the latter explained more of the variation in the timing of emergence (i.e. higher R\(^2\)), compared to the former, the trigger hypothesis was accepted. Lastly, we tested if the rate of increase in ln(CPUE) was correlated with minimum SBT.

**Bioenergetics**

In order to test the bioenergetics hypothesis, we modeled the energy reserves of overwintering sandeel and subsequently calculated the relative residual reserves (RR) as a proxy of the physiological incentive to end overwintering and start feeding:

\[
r_t = r_{t-1} - f(SBT_t, W)
\]

\[
RR = \frac{r_{t=199}}{r_{t=1}}
\]

*R\(_t\)* is the energy reserves (in Joules) in time step \(t\), and \(f(SBT_t, W)\) is the function describing the energetic cost of overwintering (Joules t\(^{-1}\)) as a function of sea bottom temperature in the daily
time step $t$ and fish weight. Daily SBT values were obtained from the same source as described above. Assuming that young of year sandeels stop feeding around 1st November the development was simulated for 199 daily time steps (i.e. from $t = 1$ to $t = 199$) corresponding to the number of days between November 1st and the day on which $A_{max}$ is reached (averaged across all years). The daily energetic cost of overwintering as a function of temperature and fish weight was modeled using the following equation adapted from van Deurs et al. (2011):

$$f(SBT_t, W) = 4.7^{(1-0.8)} \times W^{(0.8)} \times [0.08 \times SBT_t - 0.25] \times 24$$

where 4.7 is the mean weight (g) of the experimental study animals used in van Deurs et al. (2011), $W$ is the structural weight of the overwintering sandeel (g), 0.8 is the mean size-scaling coefficient of metabolism in fish (Clarke and Johnston, 1999), and the linear model inside the brackets describes the relationship with temperature. Lastly, a multiplication factor of 24 was used to match the parameterization with the daily time steps used in the present study. To account for inter-annual differences in fish weight, we used the annual mean total length ($TL$, cm) of age-0 sandeel from the annual dredge survey in November/December (using only data from DB). This survey has been running since 2004. $TL$ was subsequently converted to structural fish weight (g) using $W = 0.0019 \times TL^{3.21}$ and the initial reserve size was derived as $r_{t=1} = 0.0019 \times TL^{3.66}$ (van Deurs et al., 2011).

Lastly, we analyzed whether $RR$ explained more of the variation in $\Delta A$ and $\Delta D$, compared to temperature using simple linear regressions. Since the Danish dredge survey (from where we obtained $TL$) only dates back to 2004, the regression analyses were based on a shorter time-series (2004-2017) than the previous analyses. We therefore also repeated the previous regression analyses for minimum SBT using the shortened time-series. Furthermore, to test if $RR$ performed better than the individual parameters forcing the model (i.e. overwintering SBT and $TL$), we also analyzed the relationship between timing of emergence and $TL$ and between timing of emergence and SBT averaged across all 199 time steps used in the bioenergetics model and. The analyses were only performed for DB, as the data from this area produced the most precise GAM fits (i.e. high $R^2$) and therefore the most accurate estimates of $\Delta A$ and $\Delta D$. 


Results

Data quality

In all four areas, CPUE were, as expected, increasing initially until reaching a peak around day 140, followed by a decrease (Fig. 3). However, the shape and the precision of the GAM fits (Fig. S1-S4) differed substantially between areas and years. The overall most precise GAM fits and most distinct dome-like shapes were found in DB, whereas, the most imprecise GAM fits (i.e. noisy data) and least dome-like shape was found in ES. HR reached peak CPUE much later than all other areas and the variability around the GAM fits was high in the first half of the fishing season, whereas, data were more noisy later in the fishing season for DB and ES.

The effect of temperature and phytoplankton on the timing of emergence

The correlation between temperature (SBT and SST) and $\Delta A$ and $\Delta D$ were all negative. The correlations between SBT and $\Delta A$ were significant in at least two months in three out of four areas, indicating later emergence when the water is cold (Fig. 4). PP was only correlated with $\Delta A$ and $\Delta D$ in a few months (and very early in the year) and the correlations were positive (Fig. 4). The correlation with temperature in spring was strongest in DB. In DB, significant correlations were found for all months, except January. SBT explained on average slightly more of the variation during the first five months for significant months ($\Delta A$; $R^2 = 0.42$; $\Delta D$; $R^2 = 0.37$) compared to SST ($\Delta A$; $R^2 = 0.41$, $\Delta D$; $R^2 = 0.36$). The day of the minimum SBT was never significantly related to timing of emergence, while minimum SBT was significantly negatively correlated to both $\Delta A$ and $\Delta D$ in all areas, with the exception of $\Delta A$ in FB (Fig. 5 and 6). Minimum SBT was not correlated to the rate of increase in CPUE in any of the areas (Fig. S6).

The effect of bioenergetics on the timing of emergence

The rate of reserve depletion, predicted by the bioenergetics model, (Fig. 7A) and the predicted residual reserves ($RR$) differed substantially between years (Fig. 7B). $RR$ explained 36% and 43% of the variation in $\Delta A$ and $\Delta D$, respectively. In comparison, fish length explained slightly
more of the variation, specifically 40% ($\Delta A$) and 58% ($\Delta D$), whereas, minimum SBT explained only 17% in both cases (Fig. 8; bear in mind that the time series length is shorter here compared to figure 5 and 6). Temperature averaged across all 199 time steps used in the bioenergetics model explained as little as 6% ($\Delta A$) and 5% ($\Delta D$) of the variation.

Discussion

Monthly overages of SBT and SST and the annual minimum SBT were significantly negatively correlated with indicators of the timing of emergence ($\Delta A$ and $\Delta D$). Timing of emergence and monthly averages of phytoplankton concentrations were less correlated and the relationship positive, which was the opposite of what would be expected (i.e. high concentrations of phytoplankton in early spring was expected to promote early emergence, according to the growth hypothesis that we proposed). The day of minimum SBT showed no relationship with timing of emergence (i.e. no support for the trigger hypothesis), and the rate of the spring-time increase in CPUE did not correlate with temperature, indicating that temperature influence timing of emergence, rather than growth rate and/or emergence rate. Furthermore, based on a shorter time-series, predicted residual reserves from a simple bioenergetic model (using temperature and fish length as drivers) were able to explain the variation in the timing of emergence well (also compared to temperature by itself). This supported the bioenergetics hypothesis, except that using fish length by itself explained even more of the variance in timing of emergence.

The buildup in individual weight over the season increase by at least 60% (Rindorf et al., 2016). Hence, changes over the season in catch rates of sandeel is a measure of the combined effects of emergence and somatic growth, where the former is expected to be related mainly to temperature during the overwintering period (i.e. prior to the feeding phase) and the latter to zooplankton production and temperature during the feeding phase. The rate of increase was slightly correlated to $\Delta A$, but not $\Delta D$ (Fig. S6), indicating that the increase in weight affects $A_{\text{max}}$ (i.e. when the fish are growing fast, maximum observed CPUE is higher), but not the timing of emergence as such. Furthermore, the rate of increase was not related to temperature, which further supported that the conclusion that temperature is related to some mechanism that determines timing of emergence, whereas, inter-annual variation in growth rate is driven by other factors. These factors could be, for example, composition of the copepod community.
The temperature effect on δA was absent for FB. DB and ES showed positive correlations for the first three months of the year, whereas, the effect was observed also after March in HS. Reasons for these spatial differences may be related to the temperature response of sandeel and/or fisheries dynamics. The temperature dynamics experienced in each area vary considerably, especially the difference between SST and SBT (Fig. S7). Central regions of DB and ES follow similar trajectories, which have a non-stratified water column (i.e. SBT = SST) during winter until stratifications begins (Mar-Apr). In contrast, the shallow areas in HR experience more extreme temperatures, where stratification are present in winter/spring (SBT < SST) and late summer (SBT > SST), but not during the feeding season (Fig. S7). The colder bottom water during winter may delay emergence, but from April when the stratification breaks down and temperatures sharply increases, sandeel in HR are expected to spend more energy during the feeding season. Thus, in the absence of stratification, the night refuge in the bottom is warming up during spring and summer and the metabolic rate increase, potentially causing sandeel to extend their foraging season in order to attain large enough energy reserves to survive the next overwintering period (van Deurs et al., 2011; MacDonald et al., 2018). In terms of the GAM curves in the present study, this may result in a delayed and flatter peak in CPUE. Furthermore, if the foraging period is extended like this, catch limits may already have been reached before the peak. This notion fits well with the temperature correlations found after March in HR. To another end, deeper waters around FB experience warmer bottom temperatures (SBT > SST, Fig. S7) during winter and early spring (Nov-Mar). This may delay the effect of temperature promoting later emergence, which causes a mismatch between catches and emergence that hide any immediate effect of temperature. Some of the years excluded from the analysis due to lack of a well-defined peaks in CPUE could have been due to this, however, varying fishermen behavior and catch constraints between areas may also explain why the peaks more well-defined in some areas compared to others.

Temperature showed negative correlations with the timing of emergence for several months. Correlations with SST and SBT seemed to explain the pattern equally well. This is not surprising, because they are highly correlated. Although temperature performed better than PP in predicting sandeel emergence, the role of food availability (i.e. the growth hypothesis) should not be discarded yet (Winslade, 1974a; MacDonald et al., 2019). Large zooplankton is important for efficient foraging (van Deurs et al., 2014, 2015), where specifically two species
of Calanus play important roles for sandeel in the North Sea (van Deurs et al., 2009; Régnier et al., 2017). *C. finmarchicus* has a spring peak abundance in May coupled to deeper water areas north of the 50 m depth contour, whereas *C. helgolandicus* has a southeasterly distribution with a small spring peak but a larger maximum in autumn (Planque and Fromentin, 1996; Jónasdóttir et al., 2005). However, time-series of the prey field and feeding conditions is difficult to obtain and although the continuous plankton recorder (Lynam et al., 2013) would have been one way to approach this, deciding on which zooplankton species to include and how to weigh their relative importance was considered outside the scope of the study. Hence, only PP, as an indicator of zooplankton production, was included.

The mechanisms behind what triggers emergence and what builds up to a maximum sandeel biomass may be related. Sea temperature in March and the following spring months are closely correlated. Phytoplankton spring bloom is dependent on light and nutrients, whereas, zooplankton growth is temperature controlled (Edwards and Richardson, 2004). Higher temperature in spring may speed up copepod production and increase sandeel growth rate, resulting in an early spring peak in biomass, which could be reflected as an early peak in CPUE. However, if this mechanism was of major importance to the present results, we would have expected a positive significant relationship between the rate of increase in CPUE and temperature, but that was not what we found (Fig. S8).

The trigger hypothesis, where temperature triggers the emergence by instant stimuli was not supported by the current analysis, where no relationship was found between day of minimum SBT and timing of emergence. Instead, a negative relationship with annual minimum SBT, as well as strong correlation with SBT for several months, point towards a more gradual effect of temperature (i.e. the effect of temperature integrated over multiple months, causing the sandeel to gradually become more active). The bioenergetics hypothesis on the other hand, was better supported by the data analysis. Residual reserves (RR) that was calculated in a bioenergetics model, integrating fish length and temperature over the entire winter, indicated that during warm winters, depletion of energy reserves speed up, and because of this, emergence happens early. Several studies have provided theoretical and experimental evidence for such a relationship (van Deurs et al., 2011; Wright et al., 2017). However, since the bioenergetics model is also driven by fish length (prior to the overwintering period), we also tested the relationship between fish length and timing of emergence and found a slightly better relationship (as indicated by $R^2$) compared to using RR. Assuming that size of food matters to sandeel foraging efficiency (van Deurs et al., 2015), temperature-controlled increases in the
size of the zooplankton during spring (Carlotti and Radach, 1996) will provide increasing foraging opportunities for larger sandeel at later dates. Thus, larger sandeel may have a survival advantage of postponing emergence relative to smaller sandeel, which could explain the observed positive correlation between fish length and timing of emergence.

As an alternative explanation for the effect of temperature (i.e. not the trigger- or bioenergetics-hypothesis), Speers-Roesch et al. (2018) recently showed that cooling and to a degree darkness keeps fish in a dormant state. Both light and temperature have been shown to affect sandeel activity (Winslade, 1974b, 1974c). Thus, the observed relationship between temperature and timing of emergence could simply be due to a gradual release from a temperature-induced inactive state (Speers-Roesch et al., 2018; Silva et al., 2019).

Irrespective of what is the underlying explanation, the present study provides strong indications that temperature determine springtime emergence of sandeel. Sandeel are characterized by traits of strong site fidelity and low mobility (Gauld, 1990; Wright et al., 2000, 2019; Jensen et al., 2011). These life history characteristics make sandeel vulnerable to a changing environment. The effect of temperature have already been highlighted (Arnott and Ruxton, 2002; Lindgren et al., 2018), and shifts in important timings of life history events have been reported (Régnier et al., 2019). Counting sandeels as a central part of the food web in a future with climate change, then changes in the timing of emergence could potentially have immense ecosystem-wide consequences affecting plankton communities and predators, as well as the fisheries opportunities. Seabird community may already have responded to changes in sandeel abundance and phenology, where numerous of species have changed breeding phenology exhibiting in a later rearing period (Frederiksen et al., 2011; Burthe et al., 2012). In addition, a shift in the dominance of sandeel in the diet and altered prey selection from age-1 to age-0 individuals have been reported (Wanless et al., 2018). Furthermore, regime shifts in the North Sea zooplankton community (Beaugrand, 2004, 2009) may already have had an impact on sandeel, which have shifted from a high to a low productivity levels (Clausen et al., 2017; Henriksen et al., 2018), a trend also reflected in fisheries landings and stock assessment outputs (Engelhard et al., 2014; ICES, 2018). The causality of the exact mechanisms behind these changes are still up to debate, but shifts in the timing of emergence may be a main contributor. Also, increased warming of sandy habitats will likely increase metabolic rates during overwintering and increase diel activity in the growth season (Winslade, 1974b; van Deurs et al., 2011; Wright et al., 2017), and in combination with an earlier emergence, the forage season would be prolonged. These implications can have a range of consequences, where depletion of
energy stores and higher probability of mismatches with important prey increases predation mortality that further can compromise trade-off between energy gain and survival probability (van Deurs et al., 2010). Shifts in the timing of emergence relative to timing of the fishery may also affect fishing mortality and pose a problem to the harvest output, if the targeted biomass is comprised of smaller energy-depleted individuals with reduced economic value (Dickey-Collas et al., 2014; von Biela et al., 2019).

In summary, the relative timing of emergence was related to temperature in the North Sea. We used novel methods to describe an important life history event by using data from the fisheries to inform about the timing of emergence in sandeel. These methods can be applied to other species for which the timing of fisheries and species life history are well matched. Despite noisy data, we could obtain strong relationships that supported the notion that temperature is an important driver of the timing of emergence of sandeel after the overwintering period. The causal mechanisms involved were investigated through a series of simple linear regression models and a bioenergetics model. Both temperature by itself and when used to force the bioenergetics model (together with fish length), revealed significant relationships with temperature. However, also fish length by itself correlated to timing of emergence. Although the support for the different hypotheses proposed are inconclusive, the main part of the results leans towards an explanation related to bioenergetics somehow.

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Figure 1. Illustration of how commercial catch rates (CPUE) might inform about the biomass of sandeel. The biomass of sandeel follows a dome-shaped curve for illustration-purposes, where sandeel become available to the predators and the fishery during a feeding (and growth) period (dashed line and dashed y-axis). Sandeel biomass gradually increase as fish emerge from overwintering and start growing, and then gradually decline as feeding ceases and the sandeel once again spent more time submerged in the sand. Assuming CPUE is proportional to the biomass, it will follow a similar curve (solid line and solid y-axis). $D_0$ is the first day of fishing (a fixed day), $A_0$ is the sandeel biomass on the first day of fishing, and $A_{\text{max}}$ is the maximum biomass. The difference between $A_{\text{max}}$ and $A_0$ ($\Delta A$) were used in present study as a measure of the relative timing of emergence, where a low value indicates early emergence. Timing of emergence was also approximated by the time difference between $D_0$ and the day where 70% of $A_{\text{max}}$ is reached ($D_{70}$).
Figure 2. The four areas selected for the study (boxes). Sandeel habitats reproduced from Jensen et al. (2011) are also shown (dark grey sand banks) and catches are summed by ICES statistical rectangles (circles in the centre of each rectangle). The four study areas and the abbreviations used in the present study were Dogger Banke (DB), Elbow Spit (ES), Fiskerbanker (FB), and Horns Rev (HR).
Figure 3. Average dynamics in commercial catch rates (CPUE) over the fishing season. The figure shows the natural logarithm of daily CPUE, averaged across all years used in the study (1993-2017). The smooth trend lines were produced using general additive models.
Figure 4. Pearson correlation statistics for timing of emergence, $\Delta A$ in the left column (A) and $\Delta D$ in the right column (B), $\Delta A$ versus each of the environmental variables; sea bottom temperature (SBT), sea surface temperature (SST) and phytoplankton (PP). Color gradient represent Pearson’s correlation coefficient and significance levels are indicated by stars (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). Correlation analyses were made for each study area and each of the months from January to August.
Figure 5. Relationship between timing of emergence ($\Delta A$) and estimates of (A) annual minimum sea bottom temperature (SBT) and (B) Julian day of the minimum SBT for each study area. Lines are fitted using simple linear regressions. Explained variation ($R^2$) are provided and if the slope of a given regression line was significantly different from zero it is indicated with stars in the upper left side of the plot windows (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).
Figure 6. Relationship between timing of emergence ($\Delta D$) of (A) annual minimum sea bottom temperature (SBT) and (B) Julian day of the minimum SBT for each study area. Lines are fitted using simple linear regressions. Variation explained ($R^2$) are given and if the slope of a given regression line was significantly different from zero it is indicated with stars in the upper left side of the plot windows (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).
Figure 7. Results from the bioenergetics model. A: Predicted reserve depletion during overwintering as a function of sea bottom temperature (SBT) and time (days). Black dots and vertical dashed lines indicate position relative to the Z-axis (SBT). Only the coldest and warmest overwintering periods are shown. B: Predicted residual reserves (reserve size at any given point in time relative to the initial reserve size). Vertical dashed line indicate the point in time from where the residual reserves (RR) used in the correlation analysis was taken. The coldest and warmest overwintering periods are marked in bold.
Figure 8. Relationship between timing of emergence, ΔA in the left column (A) and ΔD in the right column (B), and three different predictors: Residual reserves on day 199 (RR), total fish length (TL) and annual minimum sea bottom temperature (SBT). Lines are fitted using simple linear regressions. Variation explained (R²) are given and if the slope of a given regression line was significantly different from zero it is indicated with stars in the upper left side of the plot windows (*p < 0.05, **p < 0.01, ***p < 0.001).
Supplementary materials

Figure S1. GAM-fits for abundances (i.e. ln(CPUE) as a function of days for Dogger Bank. Based on a number of criteria, successful (black lines) and unsuccessful (red lines) fits are shown, where only successful fits are kept in the analysis. Estimated $A_0$ and $A_{\text{max}}$ (black dots, see also Fig. 1) and $D_{70}$ (dashed vertical line) are indicated for all fits.
Figure S2. GAM-fits for abundances (i.e. ln(CPUE) as a function of days for Elbow Split. Based on a number of criteria, successful (black lines) and unsuccessful (red lines) fits are shown, where only successful fits are kept in the analysis. Estimated $A_0$ and $A_{\text{max}}$ (black dots, see also Fig. 1) and $D_{70}$ (dashed vertical line) are indicated for all fits.
Figure S3. GAM-fits for abundances (i.e. ln(CPUE) as a function of days for Horns Rev. Based on a number of criteria, successful (black lines) and unsuccessful (red lines) fits are shown, where only successful fits are kept in the analysis. Estimated $A_0$ and $A_{\text{max}}$ (black dots, see also Fig. 1) and $D_{70}$ (dashed vertical line) are indicated for all fits.
Figure S4. GAM-fits for abundances (i.e., ln(CPUE) as a function of days for Fiskebanker. Based on a number of criteria, successful (black lines) and unsuccessful (red lines) fits are shown, where only successful fits are kept in the analysis. Estimated $A_0$ and $A_{\text{max}}$ (black dots, see also Fig. 1) and $D_{70}$ (dashed vertical line) are indicated for all fits.
Figure S5. Sensitivity analysis of estimated days of timing of emergence (ΔD). Different threshold values estimated as percentage (50%, 60%, 70%, 80%, 90%) of $A_{\text{max}}$ (100%) was investigated. Boxplots (A) and Pearson’s correlation statistics are shown. Color gradient represent Pearson’s correlation coefficient and significance levels are indicated by stars (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).
Figure S6. Relationship for timing of emergence ($\Delta A$ (A) and $\Delta D$ (B)) and minimum SBT (C) as a function of the slope estimate from $A_{70}$ to $A_{\max}$. Lines are fitted using simple linear regressions. Explained variation ($R^2$) are provided, as well as Pearson’s correlation coefficient (R) and p-value (p).
Figure S7. Average monthly temperature difference ($\Delta T = \text{SST} - \text{SBT}$) for each of four areas. Grey line indicate no stratification (SST=SBT).