Distribution of Sandeel (Ammodytes sp.) in the Dutch North Sea

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Summary

Sandeels (Ammodytes sp.) are so-called forage fish. They have a crucial role in the marine ecosystem in the transfer of energy from lower trophic levels to fish, seabirds and other predators. They carry out a top-down control on zooplankton concentrations and are staple food for many bird species, many of which are currently under threat in the North Sea. They are also of commercial importance, as there is a strong fisheries on sandeel, predominantly for the fishmeal industry.

The North Sea is expected to undergo significant changes in the coming decades, due to climate change, in conjunction with the energy transition (extensive development of wind farms) and the food transition (including changes in fishing patterns). Due to the pivotal role of these fish in the food web, it is important to understand their dynamics and their habitat preference. With the exception of detailed studies in the Voordelta, habitat modelling for sandeel over the wider Dutch EEZ has not been done. In this report we present a first attempt.

Available data on the presence and absence of *Ammodytes sp.* in the Dutch EEZ and adjacent parts of the southern North Sea were compiled and used to estimate the habitat suitability for the species. Logistic regression and random forest regression methods were used to link Sandeel distributions to environmental characteristics such as bottom shear stress from currents, depth and bathymetric structures, sediment grain size composition and temperature. Presence – absence data were also overlayed with fisheries intensity data to assess the impact of bottom trawling on the presence of the species. Note, the fisheries data were data on a broad range of types of bottom trawling, not targeting sandeel.

The statistical analyses revealed the very strong dependence of sandeel on sandy substrates, even small amounts of mud (and hence a stronger consolidation of the bed) reduced habitat suitability. Because sandeel highly depends on the presence of a suitable bottom substrate, habitat destruction is one of the main threads. While there is compelling evidence of the negative effects of overfishing of the sandeel stocks, it is still unclear to what extent mortality due to non-targeted fishing or to what extent habitat destruction are an important factors.

Contents

1 Preface

In 2017, Green (2017) from the RSPB (Royal Society for the protection of birds) published an extended literature review on *Ammodytes marinus* in European waters. This was initiated by the growing concern of sandeel being an overfished stock and the consequences for the ecology of the North Sea and especially for seabirds in the UK.

In 2000, these concerns led to the closure of Scottish waters to sandeel fisheries (Greenstreet et al, 2006) and in spring 2024 the UK closed the sandeel fisheries for the Dogger Bank area. At the moment this is heavily debated and disputed between the UK and Denmark (Bounds & Foster, 2024). This illustrates the economic importance and at the same time the severity of the concerns of the consequences of overfishing sandeels.

Sandeel fisheries also takes place in the Dutch economic zone, although at a limited scale. However, in view of the ongoing infrastructural works such as sandmining and the building of windfarms, concerns are equally expressed for sandeels in Dutch waters. The debate focuses on the demonstrated importance of this stock as a food source for some bird and sea mammals species having their colonies and feeding areas in the Dutch EEZ (Aarts et al, 2019, Stienen et al, 2000). To estimate the potential impacts of above activities, knowledge about the ecology and distribution of sandeels in the Dutch EEZ is essential. To fill this gap a first analyses on distributional data and a brief overview on sandeel ecology is given in this report. For a more complete overview we would like to refer to the review of Green (2017) and the numerous other publications present of which only a part is used in this report.

There is an uneven research effort and knowledge for the different sandeel species. By far the most studied species is *Ammodytes marinus*, because of its commercial importance. Therefore most information in the scientific literature reviewed here deals with this species. Knowledge on the ecology of *A. tobianus* is more limited. This overview is therefore strongly biased but treats both species as if they have the same biology and behaviour. This is not the case and for many aspects, details on the differences between the two species are unknown. Given the mixed appearance of both species in Dutch waters, this was however the best way to give a summary of the ecological aspects and roles of sandeels in the Dutch part of the North Sea.

2 Introduction

Sandeels belong to the family Ammodytidae and are important for the food web of the North Sea (Sherman et al, 1981; Daan et al, 1990). In the Southern North Sea, three common species of Ammodytidae occur: two species of *Ammodytes* (*A. tobianus* and *A. marinus*) and the related species *Hyperoplus lanceolatus*. Besides these three species, two less common species can also be found (*Gymnammodytes semisquamatus*, *Hyperolus immaculatus* (Camphuysen and Henderson, 2017).

Adult *Hyperoplus* is relatively easy to recognize in the field, but the two *Ammodytes* species are difficult to distinguish, especially as juveniles. The same holds for the distinction between juvenile *Hyperoplus* and the two other species (See Henderson & Camphuysen, 2017). Recently molecular techniques for separating the species have been developed (Doorenspleet et al 2021; Thiel & Knebelsberger, 2016). More details, separating the three common species in Dutch waters are forthcoming in the studies of Bleijswijk et al (in prep) who developed a qPCR test to separate between the two main *Ammodytes* species and *Hyperoplus*.

Because of the difficulties in morphometric identification of the species complex, it was often not resolved at species level in historical datasets. The two species are often pooled to “*Ammodytes spp*”. In addition to this difficulty there is a confusion of common names. In literature the name “lesser sandeel” is used for *A. tobianus* as well as for *A. marinus*. Given this confusion and the incomplete identification we treat the species as a group, mainly based on their similar sediment preferences, behaviour and the fact that they are especially caught together in Dutch coastal waters.

2.1 Sandeel biology

Sandeels (*Ammodytes*) are slender elongated fishes with a maximum body length of approximately 20 cm. They have a silvery white belly and a shiny green blue or yellowish back. Dorsal fins run from a few cm behind the head to the tail. The anal fin runs over approximately the last 1/3 of the body length. The greater sandeel (*Hyperoplus lanceolatus*) can reach lengths up to 30 cm. This species has a much firmer appearance. The focus of this study lies on *A. marinus* and *A. tobianus*.

Ammodytes marinus is the off-shore species and *Ammodytes tobianus* is a more inshore species(Reay, 1973). Along the Dutch coast populations of both species mix (Tien et al, 2017). The two species differ slightly in timing of reproduction. Gonadal growth of *A. marinus* starts in September in the northern North Sea. They spawn between December and January (Bergstad et al, 2001). In western Ireland (Galway Bay) *A. tobianus* seem to have two spawning periods, *i.e.* one in spring (December-February) and one in autumn *i.e.* August-September (O’Connell and Fives, 1995). The different geographical locations might thus (partly) be a cause for the observed difference. For *A. marinus* Boulcott et al (2007) showed that there is a large regional variation in the maturation but also in fecundity (Boulcott & Wright, 2011). Gonadal maturation seems dependent on body weight and food availability. Fecundity (number of eggs) is related to body size. These findings suggest that timing of zooplankton blooms can cause large variations in sandeel growth, size frequency distributions, and maturation (Boulcott & Wright, 2008). Larger females tend to produce larger eggs (Boulcott & Wright, 2011). Development time of eggs depends on temperature (Regnier et al 2018). Within the North Sea there are different sandeel “populations” (spawning stocks) which is based on differences in growth and size at maturity (Rindorf et al, 2016) but also on modelled larval exchange (Christensen et al., 2008), and limited mixing of neighbour populations (Kunzlik et al, 1986; Laugier et al, 2015). The genetic structuring between geographically separated populations of *A. marinus* in the North Sea is weak. The occurrence of three genetic variants however suggests some reproductive isolation (Jiménez-Mena et al, 2020).

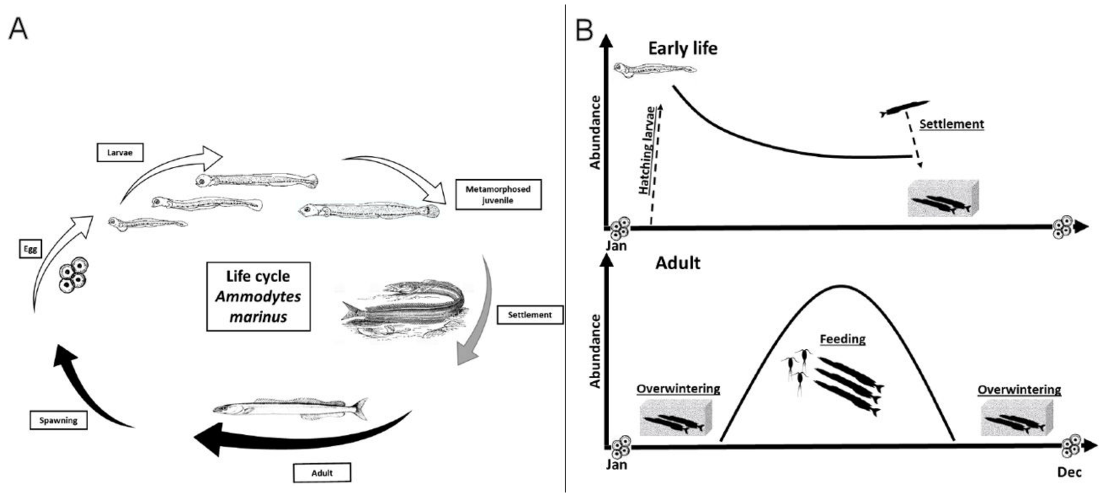

Figure 2.1: A: General life cycle of A. marinus. Early life cycle by white arrows, adult life cycle in black arrows (Henriksen et al, 2020). B: Annual shape of abundance curves of early life stages and adults (Henriksen et al, 2020)

The lifecycle of sandeel is summarized in two figures from Henriksen (2020). Figure 2.1A gives the life cycle from egg to adult and Figure 2.1B gives the lifecycle over one calendar year. Eggs are laid on the substratum where adults live. After hatching the larvae have a “drifting phase” of 1 to 3 months. For the northern and central North Sea it is likely that the larvae of *A. marinus* can drift to other adult spawning grounds as modelled by Christensen et al (2008) (Figure 2.2A). Unfortunately, their study does not give details for Dutch coastal and offshore waters where the population seems to be rather isolated. Based on hydrographical data one can assume that the population of *A. marinus* is fed by larvae from the Dogger Bank area. It is unclear to what extent the population in Dutch waters is maintained by an influx of larvae. Catch of ripe adult fish in the near coastal North Sea (Parmentier, personal communication) suggests that the Dutch population reproduces locally. It is, however, unclear how these larvae are maintained in this area as the area is dominated by a northward directed residual current, implying that locally produced larvae will end up in Danish waters. Potentially the “Dutch” populations are also fed by a larval influx from the Channel.

In the light of regional sustainability, the existence of such sub-populations has become an important issue for the management of the stock, especially because of the pivoting role of sandeel in food web of the North Sea. For the greater North Sea basin management, zones are installed aiming to regulate sandeel fisheries (Dickey-Collas, 2011). The ICES sandeel management subareas (1r-7r) is such that all of the sandeel subareas in the Dutch EEZ are part of area 1r (Figure 2.2B). This means that they are part of the Dogger Bank management area.

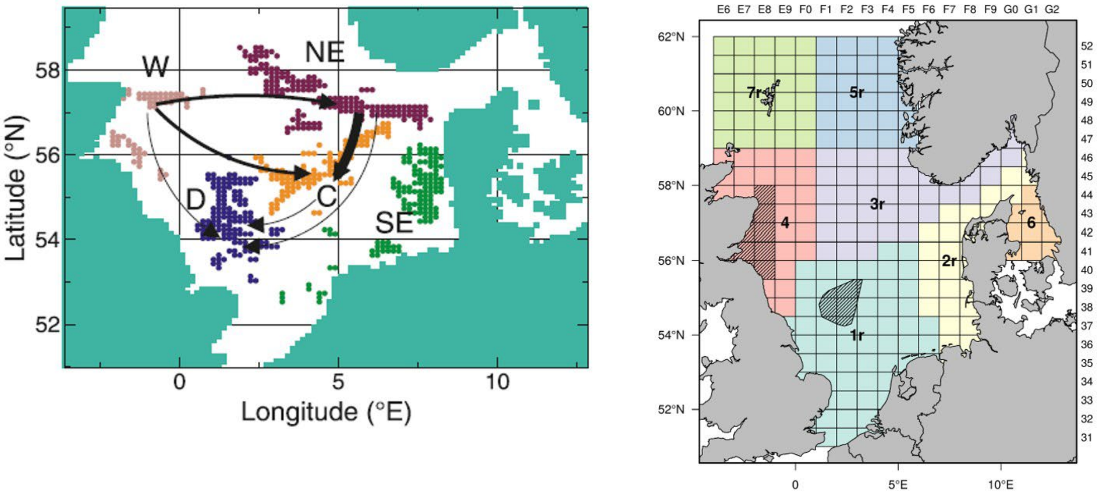

Figure 2.2: Left: Larval drift patterns and spawning stock exchange in the northern and central North Sea. From Christensen et al., 2008. Right: Sandeel management areas, (ICES, 2023)

2.2 Ecological role

Sandeels belong to the category of “Forage Fish”. These are mostly short lived (<10 yrs; Bergstad et al, 2001, Sparholt, 2015) planktivorous fish which typically have a strong schooling behaviour and can locally occur in extremely high densities. Forage fish link production at lower trophic levels directly to higher trophic levels by feeding on zooplankton and being eaten by predators. Forage fish, and sandeels especially (Otto & Opitz, 2019), exert a top down control on the zooplankton community in the southern North Sea. Their pivoting role in the food web is illustrated in Figure 2.3 taken from Otto & Opitz (2019). Sandeel populations undergo large fluctuations in recruitment. Interguild competition with herring and sprat might be an underlying cause, especially seen in the light of the intense (over) fishing of the stock. For the southern North Sea, a decreasing trend in spawning stock biomass (*A. marinus*) has been observed (Henriksen 2020).

Forage fish is used as staple food by different groups of predators including other fish (Engelhard et al, 2008), sea mammals (Aarts et al, 2018; Leopold and Meesters; 2015, Sharples et al; 2009) and birds (Furness and Tasker, 2000; Camphuysen, 2005; Embling et al, 2012; Courtens, 2017; Watanuki et al; 2008). Behaviour and distribution of predators has been proven to be linked to variations in sandeel standing stock in space and time (Herr et al, 2009; Henriksen et al, 2021b).

The important role of sandeel in the food web is illustrated by the link between the geographic locations of bird colonies and good sandeel habitats. The breeding success of kittiwakes in the north western North Sea was strongly correlated to the sandeel spawning stock biomass (Furness and Tasker, 2000; Daunt et al, 2018). A recent study (Searle et al, 2023), however, did not find evidence that fishery closure was effective for safeguarding the breeding success of auks, guillemots or puffins in the same area, suggesting that also other factors are at play, such as climate mediated changes in the pelagic food web.

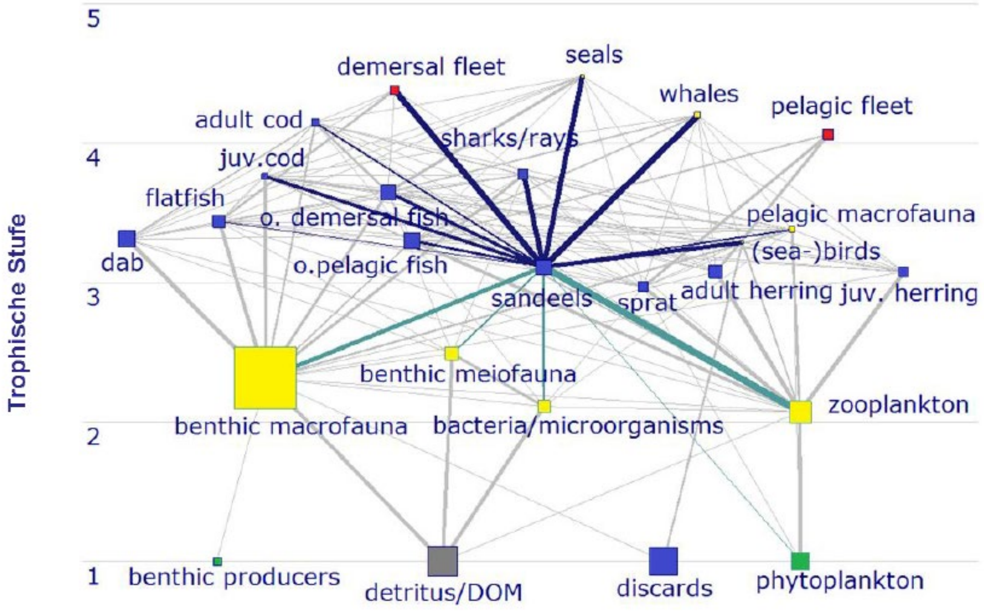

Figure 2.3: Modelled foodweb in which sandeel has a pivoting role from Otto and Opitz, 2019.

Engelhard et al (2008) showed that predatory fish in typical sandeel areas were found with more sandeel prey in their stomach. Predatory fish in good sandeel grounds had a better condition when compared to predatory fish in “poor” sandeel grounds (Engelhard et al, 2013). Links between predatory fish and sandeels were also found on a temporal scale. In good years, sandeels formed a larger fraction of the diet of predatory fish.

2.3 Behaviour & Feeding

Sandeel spend part of their life in or near the sediment. In winter, they stay permanently buried in coarse grained, silt poor sandy sediments (van der Kooy et al, 2008). The period that sandeels reside in the sediments roughly lies between August and April, based on fisheries statistics (Reay, 1970; Reeves, 1994; Henriksen, 2020). Own observations in Dutch waters with the triple-D dredge suggest that the pelagic period starts a bit earlier, *i.e.* March . The length of the overwintering period is most likely dependent on their energy reserves, the timing of plankton blooms and the onset of a developing zooplankton community (van Deurs et al, 2010; 2011). Their main prey are large copepods (van Deurs et al, 2013) but it has also been shown that they feed on herring larvae (Christensen, 2010) and most likely also on conspecifics (Eigaard et al, 2014). Once the zooplankton community has developed, sandeels start daily vertical migrations between the sediments where they reside during the night, and the water column where they feed during daylight (Winslade, 1974). These diurnal migrations have also been demonstrated in experimental setups suggesting that about 20% of the sandeels remain buried in the sediments during the day (Wright et al, 2000). According to Johnsen et al (2017), the sandeel schools stay in contact with their night time habitat by forming a collective bridging structure of fish staying in the bottom and those moving up and down wards during the day. The vertical migratory behaviour thus links night time habitat where they shelter with places where they can feed during the day (Reay, 1970). It appears that during these day-night migrations sandeels can spread up to 15 km (Engelhard et al, 2008) from their “nighttime habitats.” Jensen et al (2011) compared length frequency distributions of pelagic sandeels in and between fishing grounds and found that variation between fishing grounds was much greater than within fishing grounds. This suggests that there is limited mixing between fishing grounds, even at distances as low as 5 km. This generates a view of a high site fidelity, given the fact that sandeels burry themselves during the night. This confirms the idea by Johnsen et al (2017) of forming a living link between bottom and surface waters and not so much travel between suitable night time habitats. This is also suggested from a tagging experiment by Kunzlik et al in 1986, who found high rates of tag recaptures from grounds which were fished, while neighbouring fishing grounds did not yield recaptures. On basis of elemental fingerprinting of otoliths, Laugier et al (2015) came to the same conclusion of a high site fidelity of *A. tobianus* in the south western English Channel.

The dependence of sandeels on a specific substrate type (medium coarse sand) makes the species vulnerable to benthic habitat destruction as well as changing food conditions in the water column. Critical to their distribution is a match between bottom type and water column productivity, i.e. presence of food in the vicinity of a good sandeel bottom habitat. Such site preference marks sandeel as a central place forager. This has large implications for conservation of sandeel themselves, as well as that of other species which depend on sandeel.

2.4 Sandeel Habitat

Based on pelagic sandeel occurrence, derived from fisheries statistics, it is roughly known where hotspots of sandeel distribution are (Jensen et al, 2011). They should roughly match with bottom types that sandeels prefer. Sandeel’s nighttime and winter habitat, when they burry themselves, is “clean” coarse grained and gravely sands (Reay, 1970). This sediment preference has also been demonstrated in “choice” experiments (Wright et al, 2000). Coarse grained sediments with low silt contents are preferred (>60% 250-710µm). There might be slight differences between size classes (Wright et al, 2000). Observed ranges of preferred grainsizes differ slightly between studies (Wright et al, 2000; Reay, 1970, Holland et al, 2005) but these differences appear trivial. In coarse clean sands, sandeels are able to burry themselves quickly and once buried can breathe. Sediments with high amounts of silt (>10 %, Wright et al, 2000) and bottoms with more than 20 % fine sands (63-250µm) are avoided (Holland et al, 2005). At silt percentages between 2 and 10% densities tend to decline (Wright et al 2000). The negative relation with silt content is probably related to a reduced supply of oxygen in cohesive sediments due to low sediment permeability. Fine silt particles might also interfere (clog) with the gill function (see references in Wright et al 2000; Meyer et al., 1979). Water depth and current speeds are also factors which contribute to the explanation of sandeel occurrence. Grainsize and currents are not independent. Macer (1966) acknowledges that sandeels prefer “tidally active” areas.

Various authors modelled the presence-absence of sandeels and found that sediment grainsize, temperature and water depth can best explain their occurrence (van der Kooij et al, 2008, Zuur and Ieno *in* Tulp et al 2018). With the exception of detailed studies in the Voordelta, habitat modelling for sandeel over the wider Dutch EEZ has not been done. In this report we present a first attempt.

3 Material and methods

3.1 Sandeel in the Dutch EEZ

In this study, a first species distribution model for sandeels (*Ammodytes* + *Hyperoplus*) in the Dutch EEZ is estimated. The aim is to sketch the distribution of the species and to decipher the environmental factors that are most important to explain the distribution of the species in the Dutch EEZ.

For a first estimate of the species distribution in the Dutch EEZ, we used the workflow developed for reef-forming species in the North Sea (Herman and van Rees, 2022). We make use of environmental data collected and made available by van der Reijden et al. (2018), as well as environmental data collected by Herman and Van Rees (2022). By regressing the presence/absence data on the environmental data set, we can gain some insight in the environmental parameters steering the spatial distribution of the species, but we can also refine and improve the spatial interpolation between observations. In this analysis, we applied two regression techniques: logistic regression and random forest regression. Results of both approaches are given.

The workflow of the analysis is documented as a set of R scripts. Results are also stored as GIS files in a QGIS project. The workflow, together with the complete set of data, has been deposited in a stable repository at 4TU and is publicly available.

3.1.1 NIOZ data.

For this study we use data which are all based on sampling with the NIOZ triple D dredge (Bergman & van Santbrink, 1994). The gear is well suited to make density estimates of sparsely distributed species living in and on the seafloor. It samples bottom surfaces of 10 m² to 20 m² up to 20 cm depth over a track length of 50 to 100 m. In terms of area sampled, a typical 100 meter haul with this gear equals 260 boxcores. The long sampling trajectory reduces the effects of spatial heterogeneity on that scale. The gear only samples larger animals (>6mm) which are generally longer-lived animals better able to reflect long term trends in their environment. The net behind the dredge mouth collects the catch and has a mesh size of 7×mm 7× mm. Total volume of sand which is sampled can in principle be stored in the net. The dredge is fully quantitative because of an opening- and closing mechanism which is triggered by odometer wheels. Although there is some debate on the catch efficiency of dredges for sandeel (Johnsen & Harbitz, 2013), it appears that small benthic fish are effectively sampled with the NIOZ Triple-D dredge (Bergman & Santbrink 1994, Witbaard & Craeymeersch, 2023, Parmentier et al, in prep). Sandeels are especially well caught when buried in the bottom, during the winter months or the night. The quantitative character of the Triple-D dredge is illustrated by the generally higher abundances of small fish and benthos compared to those reported in literature.

Most sampling cruises we deal with in this report were done in the winter months. The compiled data set is therefore an effective way of estimating the spatial distribution of sandeel. Here, we utilized the Triple-D dredge data collected between 2006 and 2019 (Table 3.1). This data set holds presence absence data for 773 locations in the Dutch EEZ, all deeper than 10 meters. More recent data, in which the two *Ammodytes* species were distinguished, have not been utilized in the present analysis. At the moment a PhD (Bram Parmentier) is compiling a more complete data set, including the near coastal observations from the WMR shellfish dredge survey.

Table 3.1 Overview of the origin of the data used for the analyses in this report.

Cruise	Program	Year	Month	Startdate	Enddate	nr.hauls
64PE261	Costra2007	2007	Feb	19/02/2007	02/03/2007	64
64PE265	NZW	2007	Mar	21/03/2007	26/03/2007	14
64PE266	BSIK2007	2007	Mar-April	26/03/2007	06/04/2007	120
64PE287	Normomap2008	2008	April	05/04/2008	13/04/2008	65
64PE288	Costra2008	2008	April	14/04/2008	18/04/2008	52
64PE330	NZW	2011	Feb	18/02/2011	24/02/2011	58
64PE338	Normomap	2011	June	10/06/2011	16/06/2011	50
64PE340	NS monitoring	2011	June	17/06/2011	07/07/2011	11
64PE363	FrieseFront	2012	Nov	19/11/2012	24/11/2024	34
64PE438	NICO-10	2018	May-June	24/05/2018	06/06/2018	28
64PE463	Eels&Seals	2019	Okt	22/10/2019	29/10/2019	42
Arca2006	FrieseFront_LNV	2006	Nov	23/10/2006	27/10/2006	33
RWS31135633	MWTL-test	2018	April	09/04/2018	12/04/2018	15
RWS31144108	MWTL	2019	Feb-Mar	12/02/2019	27/03/2019	187

3.2 Environmental data

Environmental information is needed as a basis for species distribution models. For this project, we rely heavily on a recent compilation of North Sea wide environmental information by van der Reijden et al.(2018). These authors have compiled their datasets on bathymetry, grain size distribution, temperature and salinity from diverse literature sources. They have made their data available in the form of geo-tiff files, that we have downloaded for use in the present project. In the files, there is also information on bottom shear stress, but this is based on a rather coarse model. We have replaced it with results of the Deltares DCSM-FM model for the greater North Sea. The datasets used are listed in Table 3.2. Sources of the data are van der Reijden et al. (2018) for calculations of 'Bathymetric Position Index' values based on bathymetry, Stephens (2015) and Stephens and Diesing (2015) for grain size data, Copernicus marine services (www.marine.copernicus.eu) for salinity and temperature, EMODnet bathymetry (http://portal.emodnet-bathymetry.eu/) for basic bathymetry, Deltares for bottom shear stress calculated with DCSM-FM.

The 'BPI' (Bathymetric position index) calculates for each point, the difference of the depth of the point with the average depth of the surrounding area, where the surrounding area is a circle with a fixed radius. BPI5 uses 5 km as a radius for the surroundings, and similar for the other BPI variables. van der Reijden et al. (2018) also define a weighted average BPI, but we did not use that in our analysis.

Temperature difference is a measure for the change in temperature between 2008 and 2013. This is not distributed homogeneously over the North Sea. Atlantic water has warmed very little, whereas the North Sea has been warming considerably over the past decades. Consequently, the largest temperature differences are seen in the eastern and north-eastern parts of the North Sea.

No temporal (e.g. seasonal) variance of salinity and temperature has been used in the present study. It is known that variation of these variables is often very important in estuarine conditions. However, in the North Sea the ranges are much more limited.

Table 3.2 Environmental data and their source

Env.Variable	Explanation	Source
Depth	Depth at 178 m resolution	EMODnet
BPI5	Bathymetric Position Index 5 km	vdReijden, 2018
BPI10	Bathymetric Position Index 10 km	vdReijden, 2018
BPI75	Bathymetric Position Index 75 km	vdReijden, 2018
Bott.shr.stress	Bottom shear stress from currents	DCSM-FM
Salinity	Mean Salinity	Copernicus
Temperature	Mean Temperature	Copernicus
Temp.diff	Temperature Difference over the year	Copernicus
Gravel	Fraction gravel in sediment	Stephens, 2015
Mud	Fraction Mud in sediment	Stephens, 2015
Sand	Fraction Sand in sediment	Stephens, 2015

During the data exploration, it appeared that the occurrence probability of the species groups varies strongly with subtle changes in sand content between 90% and 100% of the grainsize distribution, and mud contents in the lower range between 0% and 10%. In order to better reveal these relations, the sediment fractions of sand, mud and gravel have been transformed using logit transformation. Doing so increases the resolution of the analysis near the boundaries of the distribution. A logit transformation projects data bound between 0 and 1 onto a distribution that ranges (in theory) from minus to plus infinity.

The logit transformation is defined as:

$$logit(f) = log\left(\frac{f}{1-f}\right)$$

where f is the fraction (number between 0 and 1) of one of the sediment grainsize classes, i.e. sand, mud or gravel.

3.3 Information on fisheries effort

Although fisheries intensity data were provided by van der Reijden et al. (2018), we used a more recent compilation prepared by ICES and published by EMODnet Human Use. It shows fisheries intensity estimated from VMS data in 2022. The intensity is estimated as average area swept with the subsurface part of bottom-disturbing gear types. More details on the dataset can be found in https://ows.emodnet-humanactivities.eu/geonetwork/srv/api/records/d57fbdea-489e-4e11-9ff1-f0f706cfe783

3.4 Statistical analysis

In this analysis, we applied two regression techniques: logistic regression and random forest regression. Results of both approaches are given. They are compared for unexpected deviations, that could point to flaws in the fitting.

A multivariate logistic model was fitted using the generalized linear modelling function “glm” in R, and assuming binomial distribution of the presence/absence dependent variable. Initially, all available environmental data were used in the analyses. Few factors turned out to be significant, due to strong collinearity of the responses with several of the variables. The model was reduced by addition and removal of several factors, until a model with minimal Akaike Information Criterion (AIC) was obtained. An AIC score is a number used to determine which machine learning model is optimal for describing the data with a minimum number of parameters. In the calculation of AIC the addition of extra model parameters are penalized. This prevents overfitting of the model by adding more explanatory factors. The squares of all environmental variables have been added to the model, allowing for Gaussian-type responses of the species to the environmental variable.

Random Forest models were fitted using the R package RandomForest (Liaw & Wiener, 2002). Although the dependent variable (presence/absence) is a binary variable, the Random Forest was run in regression mode, as the aim was to obtain the probability of occurrence calculated by the model. The number of variables used at each try in the random forest is a parameter that can influence the performance of the method. After extensive checking, the default number of variables (3) appeared to be the optimum and was not changed. The number of random trees generated in the forest was 1000.

For both types of models, a raster with the predictions was plotted and visually compared with the observations. The probability of finding sandeel was visualized by colour coding. At last these model predictions were visually compared with the spatial pattern in fisheries effort.

3.4.1 Data and code repository

After completion of the project, all data and scripts used in the analysis were made available from the 4TU repository (DOI: **10.4121/10afff52-4261-46b5-9a99-a1c86352bc0c)**.

In the near future, they will also be downloadable from informatiehuis marien (https://www.informatiehuismarien.nl/).

4 After completion of the project, all data and scripts used in the analysis are made available from the 4TU repository Results

4.1 Visualizing species-environment relations

As a preliminary analysis, plots are produced showing the raw data of species occurrence versus the environmental factors in the database (Figure 4.1). Sediment grain size fractions are shown both before and after logit-transformation.

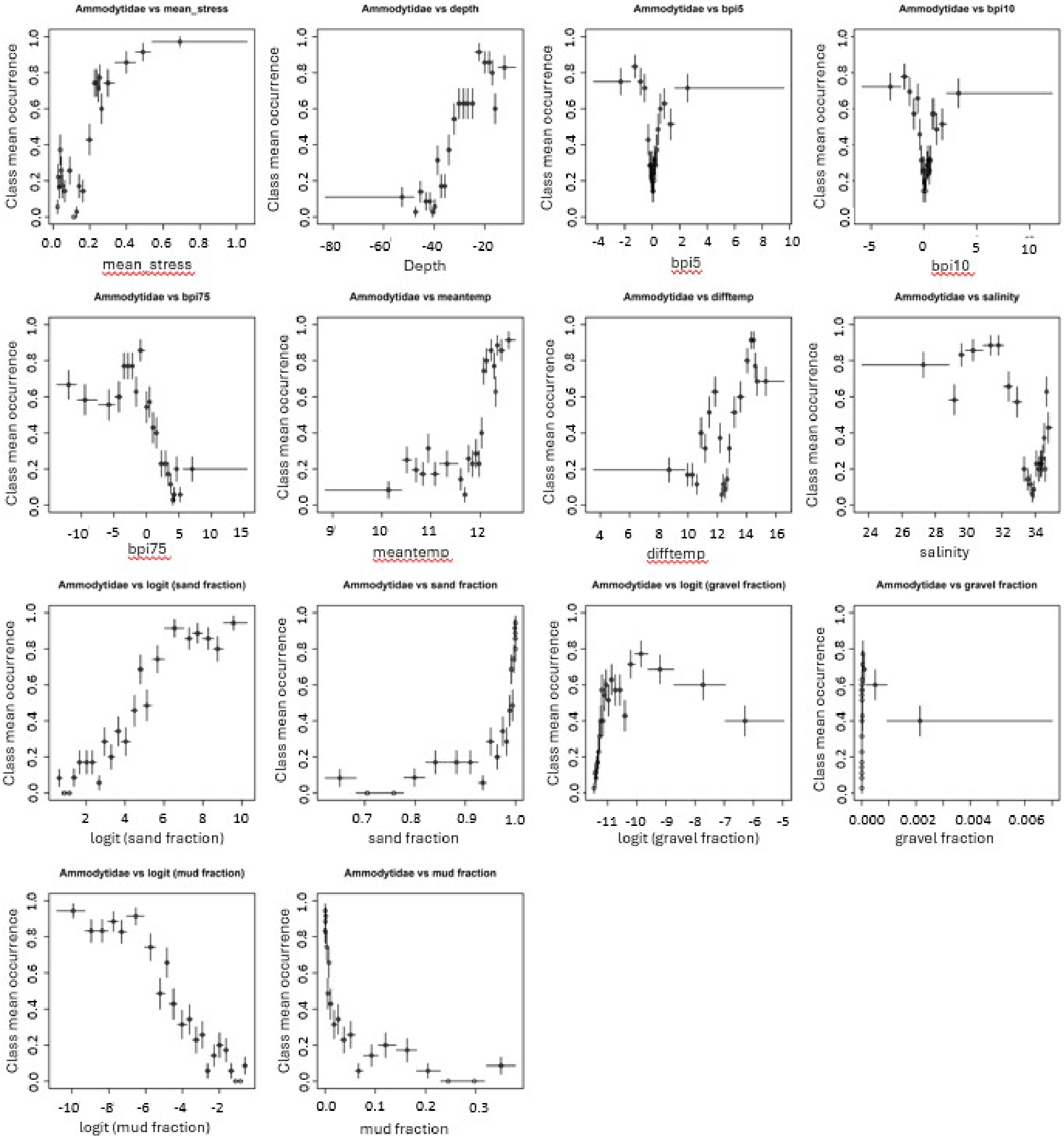

Figure 4.1: Raw plots of occurrence fraction of Ammodytidae versus environmental variables. Shown are the fraction presences per 5-percentile class of the environmental variable, across all years and spatial positions. For the sediment grain size fractions, both the logit-transformed and the untransformed environmental variables are shown.

It can be seen on the plots of Figure 4.1 that sandeels in the Dutch North Sea, prefer sites with high bottom shear stress, a depth of less than 30 m, which lie relatively close to the coast (and thus with slightly lower salinity), and a sandy substrate. When the mud fraction exceeds a level of only a few per cent of the grain size distribution, the occurrence probability of sandeels drops drastically. Occurrence probability rises sharply with a small amount of gravel, but drops at higher gravel fractions. The relations with BPI5 and BPI10 show that areas that are very flat at this scale (BPI values around zero) have lower probability of occurrence of sandeels than areas with some relief. The relation with BPI 75 follows from the fact that sandeels are mostly concentrated in the relatively shallow coastal areas, which are higher than surrounding areas at this large scale. Relations with temperature also reflect the coastal distribution of the species group.

4.2 Regression analysis

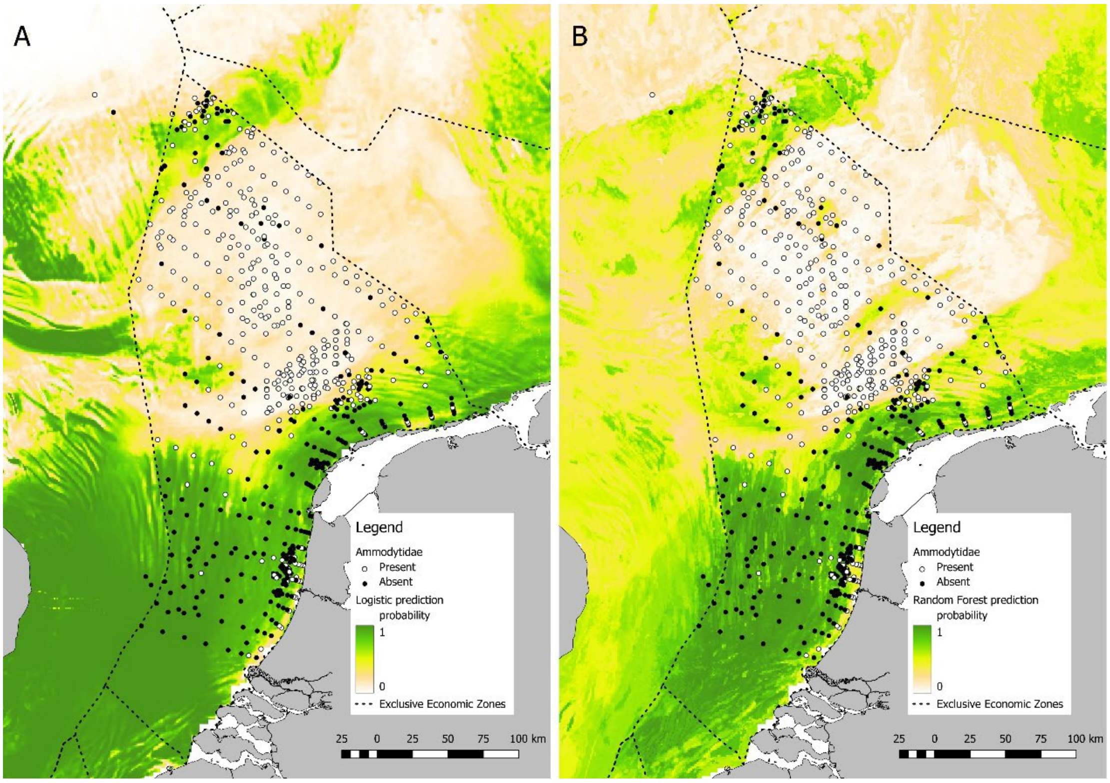

Figure 4.2: Observed occurrence of sandeels in the Dutch EEZ, and model predictions by (A) logistic regression and (B) random forest regression. White open dots indicate samples with the species absent, Black filled dots represent presence. Green-yellowish Shading represents predicted probability of occurrence from the models.

Species distribution models have been prepared with two different regression techniques: logit regression and random forest regression (Figure 4.2). For the logit regression, the environmental variables and their squared values have both been entered into the regression equation, allowing for Gaussian-type response curves. The logit regression suffered from collinearity in the independent variables. A parsimonious model has been built in order to find the model with the lowest AIC. The number of environmental variables eventually kept in the model was lower than the total number of variables available. However, the produced prediction raster was not very different between the full model using all variables, and the final model with the lowest AIC. It can be seen from Figure 4.2 that the two models do not differ very much in their overall predictions within the Dutch EEZ. However, the random forest predictions match the presence-absence more closely on a fine scale. The Dutch EEZ the only area for which data were readily available.

The general picture is that sandeels are restricted to the relatively dynamic (high bottom shear stress) and sandy areas in the shallow parts of the Dutch EEZ. Occurrence probability is low in the deeper, muddier areas. On the Dogger Bank, the occurrence probability is higher than on the deeper parts south of the Bank, but the picture is mixed and occurrence is less frequent than in the dynamic parts closer to the coast. Along the coast, sandeels are sometimes absent in the shallowest parts that are probably most exposed to wave action. The two models differ in details, e.g. in the northern delineation of the sand wave area, and distribution in the region south-east of the Cleaver Bank. Subtle differences shown in the data are, in general, better followed by the random forest model, but it is unclear whether this is a sign of overfitting or the capture of real environmental trends.

The variables retained in the logistic regression model, and their significance, are summarized in Table 4.1. Sand fraction (logit-transformed), depth and mean stress are the main factors explaining the occurrence of sandeels. However, the other factors included in the table also contributed significantly, and removal of the terms from the model resulted in higher AIC.

*Table 4.1 Variables used in the logistic regression model. For each variable, the regression coefficient and its approximate significance are given. ***: p<0.001; **: p<0.01; *: p<0.05*

terms	**coef**	**Pr**
(Intercept)	-15.0400	***
mean_stress	5.6395	***
depth	-0.2741	***
depth^2	-0.0027	**
bpi5	-0.2772	*
bpi75^2	0.0125	***
difftemp^2	0.0235	***
Sand	1.2589	***
sand^2	-0.0608	**

In random forest regression, no similar quantities to 'significance' are calculated. However, there are measures of the importance of the independent variables for the model predictions. The importance is determined by comparing the full model with a sub-model in which the values of one of the variables have been scrambled at random, and evaluating the difference in fit of both models. That can be done on the basis of the mean square error (difference between model prediction and observation), but also with a compound goodness-of-fit variable called node impurity. The results of both analysis are shown graphically in Figure 4.3.

The order of variables in both importance rankings was not always the same, but the general pattern is similar. Sand and mud fractions are very important variables, as is the level of bottom shear stress. Temperature variables, salinity and topographic indices are relatively less important, and shift place in the two rankings.

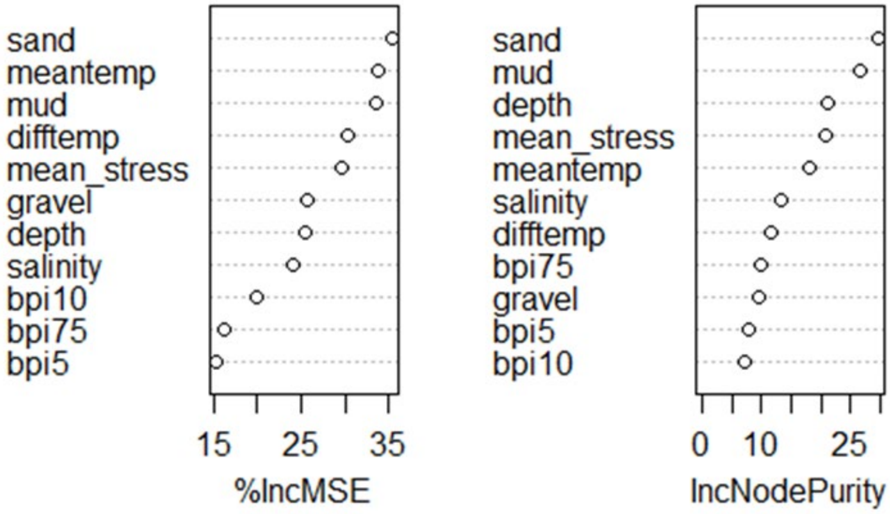

Figure 4.3: Summary of the analysis for importance of variables in the random forest model. Higher values point to more importance.

At our scale of study, no obvious relation could be seen between sandeel occurrence and intensity of bottom-disturbing fisheries (Figure 4.4). Both within the dynamic shallow area of the Dutch EEZ, and in the deep, less dynamic areas, the occurrence of sandeels is unrelated to the intensity of fisheries disturbance.

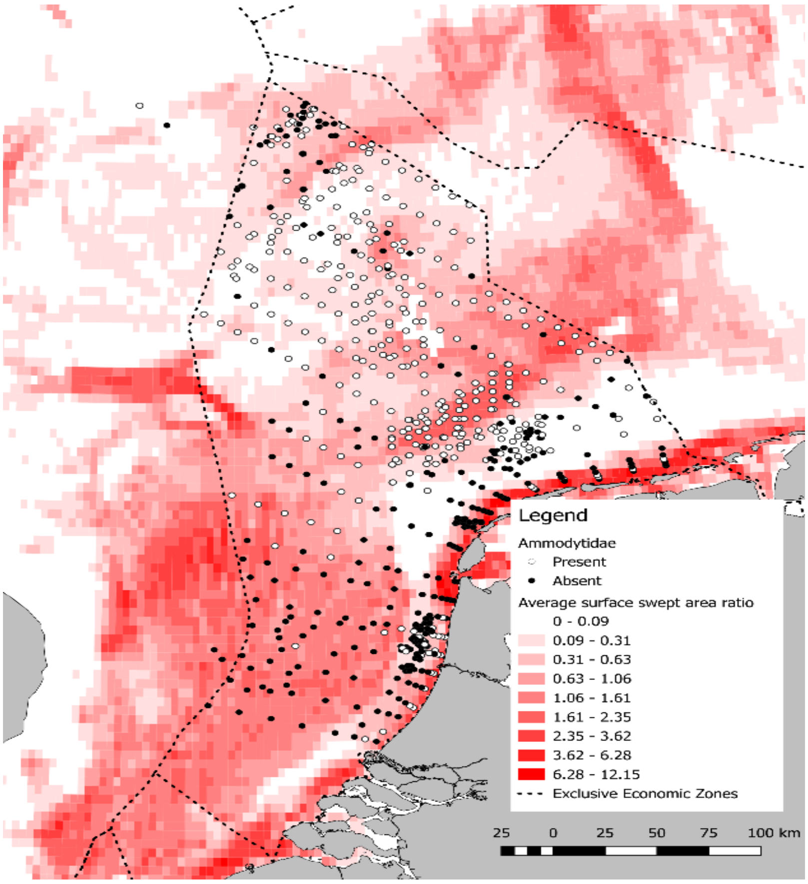

Figure 4.4 Occurrence of sandeels in the Dutch EEZ, superimposed on data of subsurface disturbance (red background colour) from fisheries. Green dots represent finds of sandeels, red dots represents absence of sandeels No obvious relation can be found between the two variables.

5 Discussion

The regression modelling, as well as the basic data exploration, showed that sandeel occurrence is strongly dependent on sediment grain size distribution. The dependence is especially steep at the very margins of the distribution of the environmental variables: between 90-100 % sand, and between 0-10 % mud. Without the logit transformation, it was not possible to correctly capture this dependence in the logistic regression model. Our results obtained from the two models, strongly support what is known from literature on the relationship between environment and sandeel occurrence. Sandeels prefer relatively dynamic and sandy areas in the shallow parts. The estimated probability of occurrence is low in the deeper, muddier areas. Topographic indices, temperature or salinity are less important factors. Sandeel abundance is inversely related to mud content in the 0-10% range, but also decreases at increasing gravel contents above a few percent (Wright et al, 2000). Along the Dutch coast there are only minor patches with gravel, but areas with considerable amounts of buried dead shell material might be present. It is likely that these have a similar effect on the probability of finding sandeel. High proportions of gravel or shells make burial more difficult but exact details are lacking. Our results corroborate the findings by Langton et al (2021) who also found a dominant effect of silt content. In contrast to our results they found that the slope of sandbanks (topographic index in our study) played a more important role. The scale over which our topographic indices have been calculated are probably too coarse to “catch” small topographic differences to which sandeel is responding.

In summary, sandeel likes to occupy clean coarse sands. In such sediment water exchange is easy so that oxygen levels of the interstitial water are sufficiently high for breathing. The important role of shear stress in explaining the observed distribution highlights the fact that sandeels prefer “tidally active areas” (Macer, 1966, Meyer et al 1979) such as edges of banks. Preferred median grainsize ranges from 250-1200 µm (Jensen, 2011, Wright et al 2000, Reay, 1970, Holland et al, 2005).

It should be kept in mind that the dataset we used is collected between the years 2006 and 2019. The samples are mainly taken during the winter period and only three subsets were collected during summer (May-June). In summer, sandeels mainly occupy the water column during daylight while also the dredge hauls are taken during daylight as these sampling campaigns were not focusing on sandeel. Sandeel could therefore have been missed from these “summer” samples, but closer inspection shows that sandeels were also found in these samples. This supports the observation that always about 20% of the population remains buried in the sediments (Wright et al, 2000). This percentage appears to be high enough to use in presence – absence modelling, although the chance of finding specimens becomes lower. Another underlying problem could be the long time period (2006-2019) over which the samples were collected. It is known that large population fluctuations occur in forage fish, but also here the presence-absence data were used and we expect the effect to be small.

6 Future of Sandeels

Since sandeels have a pivoting role in the North Sea food web, concerns have been expressed in regard to the industrial fisheries. More recently, it became clear that other anthropogenic impacts (Staudinger et al, 2020) should also be kept in mind in order not to jeopardize management and conservation goals as defined in the EU habitat directive, bird directive or the Marine Strategy Framework Directive (MSFD). The most obvious threat to sandeels is habitat degradation related to large infrastructural works like the construction of windfarms and marine deposit mining. These activities typically take place in the shallower parts of the North Sea that constitute the typical sandeel habitat. The impacts of climate on sandeel habitats should also be considered, given the tight link between the essential benthic habitat in the vicinity of good feeding grounds for sandeel. The impacts of climate change itself might also have profound effects on distribution and winter survival or indirectly by changing productivity, changing the phenology of prey and predators or causing a change in food web structure.

6.1 Sand mining & nourishments

The constant threat of sea level rise, leading to increased coastal erosion has led to the almost continuous dredging for sand along the Dutch coast for beach and fore shore nourishment. On average 10 million M^3 sand is extracted annually along the Dutch coast. The sand extraction takes place in designated areas at depths greater than 20 meters parallel to the coast. On the seaward side, the area is bounded by the 12 mile zone. Up to recently, relatively shallow (2-4 m) sandmining pits were made, but the continuous need for sand asks nowadays for middle deep (6-8 meter) sandmining. The area of sandmining along the Dutch coast overlaps with the potential habitat of sandeels. Shallow mining and nourishments lead to relatively rapid recoveries of the fauna, including sandeel. (van Hal, et al 2021). The first effect studies for middle deep sandmining (Witbaard, 2022) showed that the sandeel might avoid pits with unfavourable silty sediments as illustrated by the pit north of Ameland. Here the sandeel density outside the pit was 5 times the density of sandeels in the pit itself. The observed differences could be linked to the changes in sediment characteristics in the pit. These observations are anecdotical but they suggest that caution should be taken when sand mining takes place in sandeel habitat. The study by Witbaard and Craeymeersch (2023) suggests that middle deep sandmining might lead to an (additional) destruction of sandeel habitat by increasing silt contents in middle deep mining pits.

6.2 Wind farms

Van Duren et al (2021) performed a desk study on the potential effects of the large upscaling of offshore wind energy in the Dutch EEZ. They identified a variety of potential effects and argue that demonstratable ecosystem effects on fundamental ecosystem processes might occur. Among these are increased turbulence, change in stratification, water transparency and with that in primary production. There are however large regional differences, related to whether areas are subject to summer stratification or not.

With all uncertainties expressed in above study, the effect of windfarms on habitat suitability for sandeel, may be worrisome given the fact that “feeding” habitat and “nighttime/winter” habitat of sandeels have to match and that (planned) windfarms along the Dutch coast, partly overlap with typical sandeel bottoms. There are studies which show that the physical habitat in and around a windfarm or close to monopiles changes. The effects can be negative but also positive. The relevance of the observed changes for sandeel is however hard to estimate as illustrated in a study by van Deurs et al (2012). On the other hand, if the seabed in wind farms with suitable sandeel habitat is not changed negatively, the wind farms may also provide protection against fishing, as these areas are in general not fished by bottom trawling gear.

Coates et al (2014) studied the macrobenthic community around a monopile. They observed a change in community and fining of the sediments with an accompanied increase in sediment organic matter, especially close to the monopile. Extrapolation from one monopile to a single windfarm or a set of windfarms is hard to do, so the scale of this process remains unknown. According to the model study of Ivanov et al (2021), the effect on total organic matter deposition is considerable (50% and over wide area), but the effect of mud particle deposition is small in comparison to the fluxes related to tidal resuspension and deposition. Sandeel is however extremely sensitive to (relatively small) additions of silt and their habitat preference is inversely related to sediment silt content (Wright et al 2000; this study), thus effects on habitat suitability cannot be excluded. Windfarms also influence current velocities and turbulence intensity of the water column. This may also lead to increased concentrations of suspended matter ((5 times?) Baeye & Fettweiss, 2015) in the water column resulting in decreased water transparency. Sandeel, being an eye hunter, might suffer directly from this. Decreased transparency also influences water column productivity (Wilson & Heath, 2019) which might translate in a reduced zooplankton production as well. Increased turbulent mixing of the water column on the other hand might contribute to higher primary and secondary zooplankton production. Feeding conditions for sandeel seem critical for growth and ultimately their condition to survive the winter. The interactions of above ecosystem effects of windfarms are complex and it is difficult to estimate the effects on sandeel biology and populations. The construction of windfarms is also accompanied with a change in habitat because in an otherwise “empty” seabed, reeflike structures are built in the form of the monopiles and the stoney scour protection. These can cause a “reef effect”, introducing an additional top-down effect by increased predator abundance like cod and whiting (Lindeboom et al, 2011.) for which sandeel is an important prey. To what extent these locally elevated predator densities have a significant influence on the sandeel population is doubtful as both top down and bottom-up control of the sandeel populations has been found (Frederiksen et al 2007, Lindegren et al, 2011).

6.3 Fisheries

While sandeel is not fished for human consumption, in terms of tonnage it was the most intensely fished species in the North Sea. Since about 1950 there exists a directed fisheries for sandeels (ICES, 2010) all for industrial purposes such as oil and fishmeal. In recent decades up to 1/3 of all fish landings from the North Sea was sandeel, mostly *Ammodytes marinus*. In the late 1990ies, the annual landings surpassed a million tons (Furness, 2002; ICES, 2022). Fisheries for sandeel is well targeted and there is no evidence that this fishery disturbs the seabed in a detrimental manner (Dickey-Collas et al, 2014). Herr et al (2009) have another opinion and state that the typical sandeel habitat is particularly threatened by sandeel fisheries which might be especially true on basis of the study by Johnsen et al (2017) which show the existence of connecting structures between the bottom and schooling fish.

There is strong evidence that sandeel fisheries locally led to a collapse of the spawning stocks of sandeels, cascading through the food web up to the higher trophic levels. The spatio-temporal overlap of predators and sandeel fisheries illustrates that both are competing for the same resource. The competing effects are well documented for especially a number of seabird species in UK breeding colonies, but also from the joined occurrence of sandeel fisheries and harbour porpoises (Herr et al, 2009) and the statistical relationship between harbour porpoise occurrence and distance to sandeel fishing grounds (Gilles et al 2016)

The variation in sandeel stocks may also arise from unintended effects by commercial fisheries activities targeting other species like sole, plaice or shrimps. There are potentially two opposing effects. First the predation release by selective removal of predators like plaice, gurnard and gadoids (Engelhard, 2013) could favour sandeel survival. Secondly, commercial gears used in shrimp or flatfish fisheries can have a negative effect by habitat destruction and by raising mortality because of bycatch (Boute et al 2023).

For the Voordelta (southern Dutch coastal waters), Tien et al (2017) compared the density of all three sandeel species with fishing effort (shrimp & flatfish) in the period before sampling sandeel. They observed that all species were predominantly found at locations where the fishing effort was less and concluded that sandeel abundance was negatively affected by beam trawl and shrimp fisheries. From their study it is unclear whether this is due to increased mortality or habitat destruction but it is also possible that the spatial distribution of sandeels and fisheries exclude each other. Re-analyses of the data (Tulp et al, 2018) showed that for the lesser sandeel it was impossible to separate the effects of fisheries and other factors. The overlap between the occurrence of sandeels and fisheries was too small to arrive at a definite conclusion. On a EEZ wide scale, Figure 4.4 shows that fishing intensity and sandeel presence appear not to exclude each other but the different spatial scales for the two datasets might hide such effect. It is thus hard to tell on basis of presence absence data whether there is an effect of fisheries on sandeel abundance or not.

It is, however, evident that sandeel is among the bycatch in shrimp trawling. Glorius et al (2015) showed in an overview of bycatch in shrimp fisheries that between 22 and 100% of the hauls contained sandeels. Its effect will strongly depend on the fraction of the population fished away. For the North Sea coastal zone the average percentage hauls containing sandeels was ~ 60%. For the Wadden Sea the average percentage of hauls containing sandeels was about 45%. Again it is unclear what fraction of the sandeel population is involved and whether this bycatch has a significant effect. About 50% of the bycatch of sandeels could be categorized as discard. The other half was part of the landed catch, thus resulting in increased mortality. Mortality of the discarded sandeels is unknown which makes it hard to estimate the effect of shrimping on the sandeel population.

Sandeel spawn in their wintering habitats and eggs remain on the seafloor until they hatch. In this phase the eggs might especially be vulnerable to habitat disturbance by bottom penetrating fishing gears. It is unknown to what extent such disturbance plays a role for mortality and survival.

6.4 Climate Change

Weather and oceanographic variations and climate warming have been shown to impact primary and copepod production (Deschamps et al, 2024). Under climate warming the home ranges of fish species also change (EEA, 2024; Mohamed et al, 2023; Cornes et al, 2023). A number of fish species have undergone considerable range shifts in the North Sea. Given the necessity for sandeel to find a match between the benthic and pelagic habitat, it is unlikely that sandeel can freely adapt its home range to warming trends. Sandeels are ‘stuck’ between their feeding habitat in the water column and their benthic nighttime and overwintering habitats. Thus, the degrees of freedom for sandeel to move in response to water temperature or food source is limited. This increases their sensitivity to effects of climate change.

One well documented effect of warming trends in the North Sea are the changes in water column productivity, shifts in phenology and zooplankton community traits (Deschamps et al, 2024). These shifts have major consequences for the food conditions of planktivorous fish such as sandeel. Zooplankton productivity peaks later in the year and changed zooplankton size class distributions has consequences for the survival and growth of sandeel (van Deurs et al, 2014). Even in the absence of a direct temperature effect, sandeels will be affected by climate change.

Increasing water temperatures also directly influence sandeel. Henriksen et al (2021a) studied the effect of body size and temperature on recruitment and survival and found that in the second year of life, high bottom water temperatures correlated negatively with sandeel abundance. They also found evidence that the timing of emergence from their buried mode of life in winter, correlated with variation in bottom water temperature. Warmer years were characterized by earlier emergence (Henriksen et al, 2021b). Southerly areas, experiencing higher temperatures, showed the strongest response. This implies that a continuation of the warming trend in the North Sea might especially impact the more southern parts, i.e. Dutch, Danish and German coastal waters, roughly south of 56°N. Especially the bottom water temperature at the beginning of the overwintering period appears to be important (Henriksen et al, 2021b). Higher temperatures lead to a delay in female gonadal development, but also accelerate egg development (Wright et al 2017). This might result in phase shifts, i.e. that hatching gets out of synchrony with water column productivity as argued by MacDonald et al (2018) and van Deurs et al (2014). Higher water temperature at the beginning of the overwintering period seems to have profound effects on age-1 year class. Increased temperatures mainly have effect on individual mass and energy consumption prior to and during overwintering in the seabed. It is likely that overwintering sandeel should have a minimum condition to survive winter without feeding. Higher winter temperature leads to higher metabolic costs and thus poses an additional cost on overwintering sandeel (van Deurs et al, 2011, van Deurs et al, 2014; Boulcott and Wright, 2008).

Sandeel depends on copepod productivity in the water column. Arnott & Ruxton, (2002) demonstrated a link between the winter NAO index and recruitment in the North Sea as well as a link to Calanoid copepod abundance around the time of hatching. Variations in primary and secondary production could also explain year to year variations in year class strengths of sandeel on the Faroe Shelf (Eliasen et al, 2011). Increasing seawater temperatures and poor recruitment success of sandeels have been linked to the disappearance of the Calanoid copepod *C. finmarchicus*, a preferred food item of sandeels (van Deurs et al, 2009). There is thus strong evidence that a bottom-up control, resulting in a climate sensitivity, exists for sandeel (Lindegren et al, 2018).

7 Concluding remarks

Sandeel occupies a pivoting role in the food web. Its limited freedom in habitat choice increases its vulnerability for the combined effects of habitat destruction, overfishing and climate change. While there is compelling evidence of the negative effects of overfishing, it is still unclear to what extent mortality due to non-targeted fishing is an important factor. It has been demonstrated that middle deep sandmining along the Dutch coast gives rise to increasing mud percentages and potentially renders former habitats unsuitable for sandeels. Fining of sediments, or reef-effects of windfarms might also change habitat suitability. These processes take place on relatively small spatial scales and more pronounced and widespread effects of climate change are more likely. These exert effects over the entire North Sea and on the long term have significant effects on sandeel because of changes in the zooplankton food web, optimal temperatures for growth and development and their winter survival of sandeel.

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