

Getting to the bottom of demersal fish

Distribution, diurnal behaviour, and energetic characteristics of sandeel and other prey fishes in the Dutch North Sea

Bram Parmentier

Propositions

1. Measuring seasonal variation in the energy content of fish is crucial for assessing their quality as prey.
   (this thesis)

2. “Forage Fish” is too narrowly defined as “schooling small pelagic species”.
   (this thesis)

3. Research conducted by ship or aircraft requires a greenhouse gas emission license, similar to ethical approval of animal experiments.

4. The requirement of publishable results in PhD research discourages high-risk studies.

5. Fieldwork remains crucial for uncovering unexpected ecological connections and sparking new scientific insights.

6. Scientists do not cease to be objective scientists when they become activists.

7. Weak international laws undermine global ocean protection.

8. Society allocates more attention to individual animal tragedies than to the broader ecological picture.

Propositions belonging to the thesis, entitled: ‘Getting to the bottom of demersal fish - Distribution, diurnal behaviour, and energetic characteristics of sandeel and other prey fishes in the Dutch North Sea’

Bram Parmentier
Wageningen, 7 October 2026

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General Introduction

Bram Parmentier

1. FISH AS FOOD FOR PREDATORS

Resources, either abiotic or biotic, are key factors shaping the foraging behaviour and distribution of predator species (Benoit-Bird et al., 2013; Fauchald, 2009; Sveegaard et al., 2012). An important biotic resource for a wide range of marine (top) predators is small fish, as they form a major component of their diet. Despite their importance, knowledge of small fish, including their (absolute) abundances, small-scale spatial distributions, temporal trends, and behaviour, remains limited. Consequently, this constrains the ability to interpret predator behaviour and population dynamics.

"Small fish" are defined as fish smaller than 30 cm (Daan et al., 2005; Rogers & Ellis, 2000), a size class that represents prey for many predator species (Aarts et al., 2019). The small-fish category includes both juveniles of larger species and small-bodied species, encompassing both demersal and pelagic fish. Pelagic small fish inhabit the open water column in schools and include species such as herring, sprat, sardine, and anchovy, often referred to as "forage fish" because they are considered as typical prey for many predator species (Cury et al., 2000; Engelhard et al., 2014; Pikitch et al., 2014). Demersal species inhabit the zone near the seabed and can be divided into benthic and benthopelagic species (Bergstad, 2009). Benthic fish, such as flatfish species, skates, dragonets, and gobies, rest on or burrow into the substrate due to their negative buoyancy resulting from the absence of a swim bladder. Benthopelagic fish, including cod, mullets, and whiting, swim above the seabed but remain associated with the bottom and can also enter the open water column. Sandeel (Ammodytidae) span both groups: they enter the open water column to forage, but they also burrow into the sediment. In this thesis, the focus is on buried sandeel, alongside other small demersal fish species, in their role as prey for (top) predators.

In the North Sea, sandeel is regarded as the most important prey fish species due to its high abundances, with estimates suggesting they comprise ~25% of the total fish biomass (Christensen et al., 2013), and availability to both benthic and pelagic predators (Engelhard et al., 2014). Seabird species, including guillemot, razorbill, and kittiwake, direct their foraging trips towards areas with high sandeel abundance (Camphuysen, 2005; Carroll et al., 2017; Wanless et al., 1998). Similarly, the presence of marine mammals such as minke whale, as well as the foraging movements of grey seal, have been shown to overlap with areas of high sandeel densities (Macdougall & Robinson, 2025; McConnell et al., 1999). The spatial distribution of predatory fish such as haddock and whiting has also been positively correlated to areas where sandeel are present (Temming et al., 2004).

Beyond these spatial links, dietary studies further highlight the importance of sandeel as a key prey resource. For example, sandeel make up approximately 65% of the diet of common guillemot chicks in the UK (Anderson et al., 2014), and 20-60% of the diet of breeding sandwich terns in Belgium and southern part of the Netherlands (Courtens et al., 2017). For several piscivorous fish species (plaice, haddock, whiting, turbot, grey gurnard, and greater sandeel), sandeel is the primary food source, comprising at least 30% of their diet by mass (Ludwig et al., 2024). In the UK, sandeel make up approximately 75% of the diet of harbour seal (Sharples et al., 2009). In the Dutch North Sea, this proportion is considerably lower, accounting for about 18% of the diet by mass, although it reaches around 30% when expressed in terms of prey counts (Aarts et al., 2019). A similar proportion (18% by mass) is also observed in harbour porpoise in this area (Leopold, 2015). In the Norwegian part of the North Sea, sandeel have become an increasingly important prey item for harbour seal, with their contribution rising from 12% to 40% between 1977 and 2020 (Kappa et al., 2026). A similar trend is observed for piscivorous fish in the western North Sea, where sandeel became an increasingly important component of their diet (Hunt et al., 2025).

Dependence on sandeel is also reflected in predator body condition. Body condition of whiting, lesser weever, grey gurnard, plaice, and haddock is higher in areas or during years of increased sandeel abundance (Engelhard et al., 2013). Conversely, starvation in harbour porpoise has been linked to reduced sandeel consumption (MacLeod et al., 2007). Similarly, declining breeding success in several seabird species has been associated with localised low sandeel availability (Régnier et al., 2024; Searle et al., 2023). Such effects may also scale up to the population level; for example, harbour seal populations have declined in regions experiencing reductions in sandeel abundance (Wilson & Hammond, 2019).

The localised reductions in sandeel abundance may in part result from sandeel fisheries (Frederiksen et al., 2007; Rindorf et al., 2000; Searle et al., 2023). The sandeel fishery season runs from April to the end of July, although it is shorter in Norwegian waters (ICES, 2024a). Sandeel is mainly caught using a bottom otter trawl with a small (16 mm) mesh size (Ovegård & Valentinsson, 2026) and are primarily targeted by Danish and Norwegian industrial fisheries for the production of fish oil and fishmeal (Furness, 2002; ICES, 2024a, 2025a). The fishery represents a large industry, with sandeel among the top-harvested fish in the North Sea (ICES, 2025a). Between 1980 and the early 2000s, landings exceeded one million tons annually, whereas over the last 20 years, landings have ranged between 200,000 and 500,000 tons (ICES, 2025a). The removal of such large

quantities raised concerns about reduced seabird breeding success along the Scottish coast, particularly in the Firth of Forth area, which contributed to the closure of the fishery there in the early 2000s (Daunt et al., 2008; Frederiksen et al., 2007; Rindorf et al., 2000). This closure was positively associated with breeding success in kittiwake; however, similar effects were not observed for other seabird species (Searle et al., 2023). More recently, ongoing concerns for seabird populations and wider ecosystem effects led to the closure of the sandeel fishery on the Dogger Bank in 2022 (ICES, 2026a; Searle et al., 2023). This was followed by a closure of the entire UK Exclusive Economic Zone (EEZ) in 2024 to sandeel fisheries (ICES, 2026a).

Alongside sandeel, other small demersal fish are additionally important as prey for predators in the North Sea. For example, goby (Gobiidae) make up (based on counts) 19% of the diet of harbour seal and 82% of the diet of harbour porpoise in the Dutch coastal zone (Aarts et al., 2019; Leopold, 2015). Several other small demersal species likewise serve as key prey for those marine mammals, including juvenile flatfish such as sole and plaice, the small-bodied flatfish species scaldfish and solenette, and roundfish such as rockling (Lotidae) and whiting (Aarts et al., 2019; Leopold, 2015). Small demersal species are also frequently consumed by piscivorous fish such as cod and grey gurnard (Hunt et al., 2025; Ludwig et al., 2024). Similarly, seabirds consume many small demersal species, for instance, cormorant and shag feed largely on (juvenile) flatfish and goby (Howells et al., 2019; Leopold et al., 1998; van Rijn & van Eerden, 2021). Nevertheless, it remains unclear whether top predators in the North Sea actively target areas with high densities of a particular small demersal species (excluding sandeel), or whether they prey on such species opportunistically.

Because small fish are key prey for predators, understanding their distribution and abundance is essential. Accurate knowledge of where and in what numbers prey species occur helps in understanding foraging behaviour and spatial distribution of top predators, including their feeding choices. However, such information is largely lacking in the Dutch North Sea (Madden et al., 2025). Without it, interpreting predator behaviour or assessing how spatial and temporal changes in prey availability affect the wider ecosystem remains challenging.

2. STUDY SPECIES

This thesis focuses on small demersal fish, with a particular emphasis on sandeel. A brief overview of their main characteristics in the study area is provided below.

Sandeel (Ammodytidae)

Sandeels comprise 34 species globally across seven genera, of which *Ammodytes*, *Gymnodytes*, and *Hyperoplus* occur in the North Sea (Froese & Pauly, 2025; Heessen et al., 2015). Along the Dutch coastal zone, three species are commonly found: lesser sandeel (*Ammodytes marinus*), small sandeel (*Ammodytes tobianus*), and greater sandeel (*Hyperoplus lanceolatus*) (Tien et al., 2017; van Hal et al., 2021). Those species (see Fig. 1) can be distinguished based on morphological characteristics such as whether the premaxillae are protrusible, presence of vomerine teeth or dark spot on nose, and caudal fin characteristics. However, accurately distinguishing *A. marinus* and *A. tobianus* is challenging (Heessen et al., 2015; Nævdal & Thorkildsen, 2002). In terms of spatial distribution, *A. marinus* generally occurs further offshore, whereas *A. tobianus* is typically found closer to shore, although their distributions overlap along the Dutch coast (Tien et al., 2017; van Deurs et al., 2012; van Hal et al., 2021). *H. lanceolatus* is not strongly associated with either offshore or nearshore habitats and occurs in relatively low numbers compared to the *Ammodytes* species.



Figure 1: The three most abundant sandeel species in the Dutch EEZ. Photographs by Bram Couperus (WMR).

Sandeel (Ammodytidae) are elongated fish with a characteristic semi-pelagic behaviour, which exhibits both diurnal and seasonal vertical migration patterns between the water column and bottom. During the productive spring and summer months, sandeel forage on zooplankton in the water column during the day, while at night they are burrowed in the seabed (Engelhard et al., 2008; Freeman et al., 2004; Henriksen et al., 2021; Winslade, 1974a). In the water column, sandeel are visual feeders that primarily feed on zooplankton such as copepods, although *H. lanceolatus* also target juvenile fish, including sandeel (Macer, 1966; O'Connell & Fives, 1995; van Deurs et al., 2013). The daily movement patterns are also reflected in predator behaviour. For example, sandwich terns primarily feed sandeel to their chicks around noon, whereas towards the evening they bring relatively more clupeids (Stienen et al., 2000). This prey choice seems a reflection of sandeel availability in the water column. Similarly, stomach content analyses of whiting and haddock show rapid increases in the proportion of sandeel during the night, indicating that those predators were targeting burying sandeel (Temming et al., 2004). Another example where prey availability determines the food choice of the predator.

In addition to their daily vertical migrations during summer, sandeel remain buried both day and night in the seabed during the autumn and winter months (van Deurs et al., 2010). This strategy is thought to conserve energy during periods of low food availability, as zooplankton is not present and swimming is energetically costly due to the absence of a swim bladder. Hiding (by burial) is thought to reduce predation risk during non-feeding periods (Reay, 1970; Wright et al., 2000). However, with ongoing ocean warming, this energy-saving strategy may become increasingly costly, as metabolic rates rise with temperature (van Deurs & Hartvig, 2011).

The seasonal differences in seabed presence are also reflected in the diets of top predators. For example, the proportion of sandeel in seal diet is lower during summer than in winter (Sharples et al., 2009), suggesting that seal primarily target sandeel when they are buried in the seabed. Harbour porpoise exhibit similar foraging behaviour by targeting sandeel in the sediment, with more than 40,000 pits of approximately 11 cm depth observed in the German Bight of the North Sea (Schneider von Deimling et al., 2023).

Sandeel themselves typically bury 1–4 cm into the sediment (Behrens, et al., 2007). They prefer clean, coarse-grained, silt-poor, and well-oxygenated sand, which ensures adequate oxygen supply and prevents clogging of their gills (Henriksen et al., 2024; Holland et al., 2005; Langton et al., 2021; Reay, 1970; Tien et al., 2017; Wright et al., 2000). Given this strong substrate preference, sandeel

are closely associated with sandbanks across the North Sea, with particularly high densities on the Dogger Bank (Jensen et al., 2011; Langton et al., 2021). They exhibit high site fidelity to their burrowing habitat, as their daily movements are generally limited to a few kilometres around these burrowing areas (van der Kooij et al., 2008; Wright et al., 2019). Their strong habitat preference and high site fidelity make sandeel a predictable food source for predators and a reliable target for fisheries. However, it also renders them particularly vulnerable to local depletion and habitat changes, such as silting of sand-extraction pits.

In addition to burrowing in the seabed, sandeel attach their demersal eggs to the substrate, where they hatch after approximately 1–3 months (Wright & Bailey, 1996). The larvae subsequently drift in the water column until metamorphosis into juveniles, after which they settle and burrow into suitable sandy substrates (Christensen et al., 2008). Sandeel (*A. marinus)* larvae settling in the Dutch coastal zone are transported from Belgian waters in a north-easterly direction (ICES, 2023a). The exact timing of spawning events is species-specific: *A. marinus* spawns in midwinter, whereas *A. tobianus* exhibits two spawning periods, in autumn and spring (Bergstad et al., 2001; Reay, 1970). Although the general biology of sandeel in the North Sea is relatively well understood, detailed species-specific knowledge in the Dutch EEZ—including their spatial distributions or spawning locations—remains limited.

Other demersal species

Besides sandeel, other small-bodied demersal fish that are mainly found in the southern North Sea include dragonets (Callionymidae), solenette, scaldfish, and gobies (Gobiidae) (Callaway et al., 2002; Heessen et al., 2015). Gobies comprise many species, but in the Dutch part of the North Sea the genus *Pomatoschistus* predominates (Heessen et al., 2015). *Pomatoschistus* are mainly distributed along the coastal zone from the Netherlands to Denmark (Heessen et al., 2015), and since the 1970's gradually increasing in abundance (Tulp et al., 2008). A similar increase has been observed for dragonet (C*allionymus lyra* and C*allionymus reticulatus)* solenette, and scaldfish (Tulp et al., 2008; van Hal et al., 2010). As these species are considered Lusitanian, or warm-water-preferring species, their increasing abundance has been associated with warming of the North Sea (Jones et al., 2023; van Hal et al., 2010). In addition juveniles of boreal and commercially important species such as sole, plaice, and dab are also common (Bolle et al., 1994; Reiss et al., 2010). These species have also been affected by environmental change, showing declines in maximum body size over the past century, due to a combination of sea warming and size-selective fishing pressure (Baudron et al., 2014; Tu et al., 2018). However, larger adults can still exceed 30 cm, so only the younger individuals can be considered as 'small fish'. Thus,

while general trends for small demersal fish are documented, fine-scale, absolute species-specific abundance estimates in the Dutch EEZ are still lacking.

3. SURVEYING SMALL DEMERSAL FISH

Fishing is currently still the primary method for assessing demersal fish communities. Newer and less detrimental techniques such as eDNA, camera surveys, and passive acoustics are increasingly used, though they do not replace traditional fishing. One reason is the need to maintain long-term datasets that allow consistent comparisons over time and space. Moreover, fishing provides essential biological information, such as age from otoliths, sex, size at maturity, and length–weight relationships, all of which cannot currently be obtained using non-capture methods.

In the North Sea, demersal fish communities are monitored through several surveys coordinated by the International Council for the Exploration of the Sea (ICES). In the Dutch area, the offshore (>20 m depth) area is surveyed through two survey programmes (Fig. 2a). The Beam Trawl Survey (BTS) targets fish living directly on the seabed using a beam trawl. The second survey, the International Bottom Trawl Survey (IBTS), employs a Grande Ouverture Verticale (GOV) otter trawl, which captures swimming fish up to several metres above the seafloor. These ICES surveys are primarily designed to collect data (e.g. abundance, distribution, biological parameters) to conduct stock assessments capturing (relative) annual trends of commercial importance fish species (ICES, 2022). As a result, both surveys sample small demersal fish inefficiently due to either the large mesh sizes (40 mm for BTS) or the relatively loose seabed contact (the GOV trawl) (Knijn et al., 1993). Furthermore, both surveys do not cover the near-coastal zone (<20 m).

To cover the near-coastal zone, two additional inshore surveys are conducted. The Sole Net Survey (SNS) samples along transects across and perpendicular to the coastal zone (Fig. 2a). The survey primarily targets intermediate-sized flatfish, but still uses a 40 mm mesh (ICES, 2024b). The Demersal Fish Survey (DFS) employs a finer 20 mm mesh to capture small demersal fish, with a particular focus on juvenile flatfish (van Beek, 1997). The DFS catches small species more efficiently than the offshore surveys, but still, the numbers of fish caught in the fishing path remains low, ranging from 10–40% (Aarts et al., 2019) of what is present. Catch efficiency for sandeel is even lower in demersal surveys due to their burrowing behaviour and slender body shape (Jensen et al., 2011).

To address the catch limitations of standard demersal surveys in sandeel stock assessment, a North Sea–wide monitoring programme—the North Sea Sandeel Survey (NSSS)—is conducted. Within the Dutch North Sea, however, only three sampling locations were covered initially, beginning in 2012, including the Dogger Bank (Fig. 2b). From 2017, five additional locations closer to the Dutch coast were added, but overall spatial coverage remains limited and is restricted to known sandeel fishing grounds. In addition, the dredge used in this survey has a relatively low catchability of approximately 5% (Johnsen & Harbitz, 2013), therefore the NSSS is primarily suitable for detecting interannual trends and collecting biologically relevant information.

Using acoustic methods, as done for other pelagic species, to estimate sandeel population abundances is also difficult, as a proportion of the population remains buried in the sediment even during foraging periods. This proportion varies with environmental conditions, such as water temperature and light levels, and differs among age classes, introducing uncertainty in acoustic abundance estimates (Greenstreet et al., 2006).

4. ALTERNATIVE SURVEY METHODS

To overcome the limitations of the standard annual ICES surveys, particularly low catchability of small demersal fish and limited spatial coverage, this thesis analyses data from two alternative survey methods. The first method employed the NIOZ Triple-D (Deep Digging Dredge; picture at page 19). This gear was originally designed to quantitatively sample macrobenthos and is equipped with a fine mesh size (7 × 7 mm; Bergman & van Santbrink, 1994; Witbaard et al., 2013). The Triple-D captures organisms up to 20 cm above the sediment and has a 20 cm wide cutting blade that penetrates 20 cm into the seabed. The sediment penetrating blade enables the capture of burrowing fish, including sandeel. For this study, five dedicated surveys were conducted between 2019 and 2023, including a multidisciplinary cruise to the UK Dogger Bank in the summer of 2023 (Fig. 2c). In addition, data collected since 2006 were obtained from other projects.

The second method consisted of a dredge-based survey, the Dutch Annual Shellfish Survey, which monitors shellfish (bivalves) in the Dutch coastal zone (<12 nm; Fig. 2c). It is commissioned by the Dutch government under the statutory research tasks programme (''Wettelijke Onderzoekstaken'', WOT) and conducted by WMR. The dredge (picture at page 20) used in this survey has a 9–10 cm wide blade (depending on the specific blade used) that penetrates

10 cm into the sediment. Catches are sieved over a 5 mm mesh (Troost et al., 2021). The combination of sediment penetration and fine mesh makes the survey well suited for capturing sandeel as well. Additionally, because the survey covers the coastal zone, it provides a unique opportunity to investigate differences in habitat preferences between the two *Ammodytes* species co-occurring in the area. Furthermore, as the survey is conducted during daytime in spring, it offers insights into the diurnal behaviour of sandeel during the spring months. In this thesis, data from the shellfish survey for the years 2016–2018 and 2020–2022 were analysed.

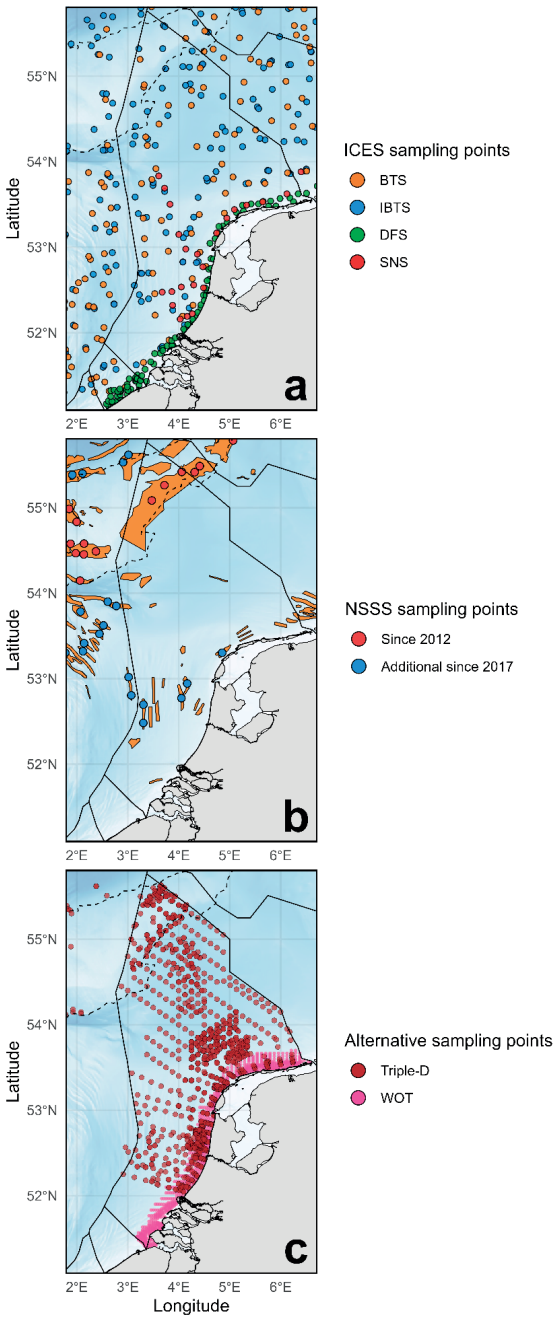


Figure 2: a) Sampling locations of the standard annual demersal surveys conducted in the Dutch EEZ. b) Sampling locations of the sandeel-specific North Sea Sandeel Survey (NSSS), with initial sites sampled from 2012 and additional locations added from 2017 onwards. Orange polygons indicate known sandeel fishing grounds (Jensen et al., 2011). c) Sampling locations of the alternative survey data analysed in this thesis. In all three panels, the Exclusive Economic Zones (EEZs) and the 30 m depth contour at the Dogger Bank are indicated.



Overview picture of the Triple-D at night at the Dogger Bank in the summer of 2023.



Overview picture of the WOT dredge.

5. THESIS AIM

Although small demersal fish play a key role as prey in the southern North Sea ecosystem, fundamental knowledge of their (spatial) ecology remains limited due to the challenges of quantifying them with standard surveys. As a result, small scale species-specific spatial distributions and biomass estimates of these key prey fish are lacking, also in the Dutch North Sea (Madden et al., 2025). Consequently, studies often rely on proxies to infer predator foraging behaviour (e.g. Fijn et al., 2022), face substantial uncertainty in estimates of prey availability (e.g. Aarts et al., 2019), or omit prey availability altogether (e.g. IJsseldijk et al., 2021). Therefore, questions such as whether harbour seal populations in the southern North Sea are experiencing food limitation remain difficult to answer (Galatius et al., 2025). Beyond gaps in (absolute) distribution data, (seasonal) energy densities and prey-specific behaviour and its potential influence on predator foraging choices also remain poorly understood in the Dutch North Sea (Madden et al., 2025).

The main objective of this thesis is therefore to enhance understanding of multiple aspects of prey availability, including the spatial distribution, abundance, energetic content, and (diurnal) behaviour of small demersal fish, with a particular focus on the two most abundant sandeel species (*A. marinus* and *A. tobianus*) in the Dutch North Sea. Such knowledge is essential for interpreting the foraging behaviour and spatial distribution of (top) predators. By meeting the main objective, this thesis establishes a quantitative baseline for small demersal fish communities, providing a reference point for monitoring and interpreting future changes due to climate change and other anthropogenic influences. Accordingly, the following main research question was formulated: **What are the distributional, energetic, and (diurnal) behavioural characteristics of small demersal fish, particularly the two *Ammodytes* species, in the southern North Sea?** This main question is addressed through the following sub-questions:

- What are the spatial distributions, in terms of both biomass and energy density, of the most abundant small demersal fish, as well as of the entire aggregation of all small demersal fish?
- Do the two *Ammodytes* species play different roles as prey in the ecosystem?
    - Which factors affect their spatial distributions and do they differ?
    - Do they exhibit different vertical migratory behaviours, either during the day or throughout the foraging season?
    - Do they differ in energy content throughout the season?

6. OUTLINE AND APPROACH

The thesis is structured to address the main research question regarding small demersal fish in the southern North Sea. A graphic overview of the different research chapters is given in Figure 3.

Using the Triple-D data, **Chapter 2** presents spatial distributions for the seven most abundant small demersal fish (based on biomass) species as well as their total aggregated biomass distribution. To assess the efficiency of the Triple-D fishing gear, biomass estimates were compared with those obtained using other demersal fishing gears.

Alongside the assessment of prey quantity in Chapter 2, prey quality is considered an additional key factor influencing predator foraging behaviour (Spitz et al., 2012). **Chapter 3** therefore quantifies seasonal and species-specific differences in energy density, with particular focus on comparisons between the two *Ammodytes* species. The energy density estimates are subsequently combined with the biomass distribution maps from Chapter 2 to generate spatially explicit energy landscapes.

As mentioned earlier, the two *Ammodytes* species are morphologically difficult to distinguish with certainty (Heessen et al., 2015; Nævdal & Thorkildsen, 2002). Therefore, newly designed species-specific DNA primers, as well as a primer for identifying *H. lanceolatus*, were developed to enable a reliable and cost-effective DNA identification method. **Chapter 4** describes the development and evaluation of primers, alongside an assessment of morphological identification. Individuals identified to species level using this method were subsequently used to distinguish between *Ammodytes* species in Chapter 3, while DNA-identified individuals were additionally used to complement morphological identification in species-specific analyses in Chapter 5.

Chapter 5 investigates species-specific differences in burrowing habitat between the two *Ammodytes* species in the Dutch coastal zone. The dataset also allowed us to examine the relationship between bivalve and sandeel densities. In addition, species-specific behavioural patterns, both diel and seasonal, were inferred from variation in *Ammodytes* densities in the seabed.

In **Chapter 6** I synthesise the results of the research chapters and highlight the main findings. I further outline recommendations for future research, including how to link the results to (top) predators that depend on small demersal fish,

and discuss why this, including human influence, is important for improving the ecological status of the southern North Sea ecosystem.

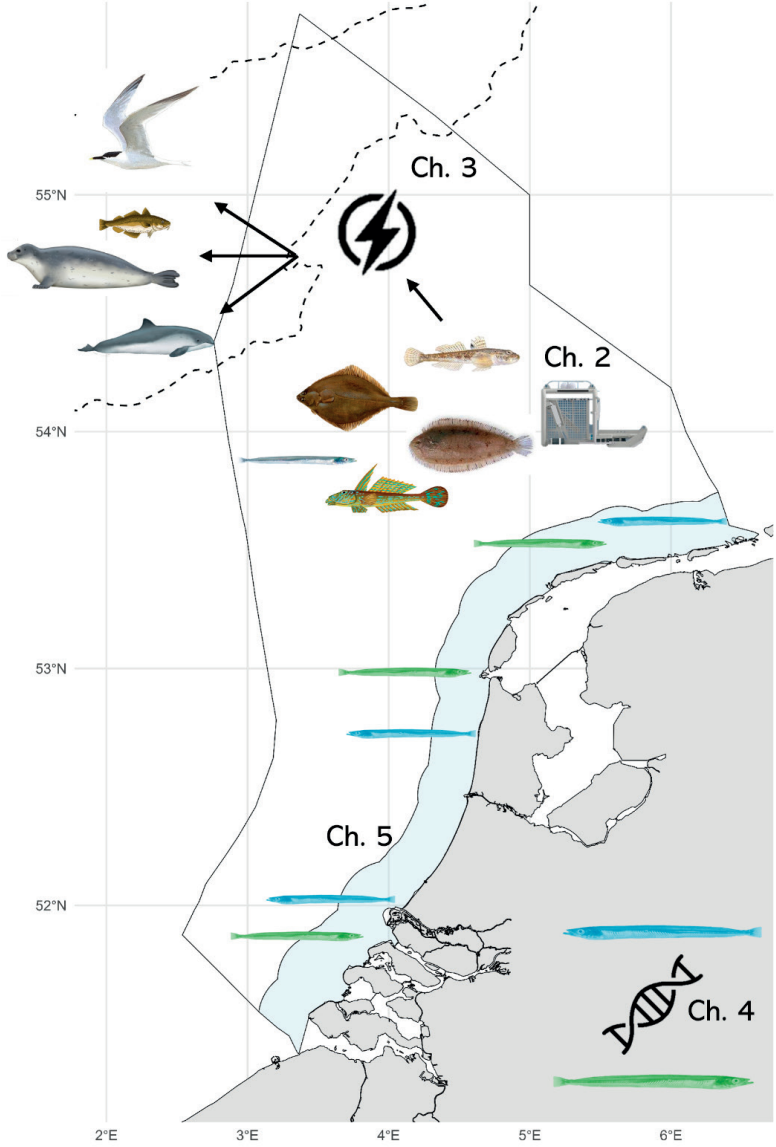
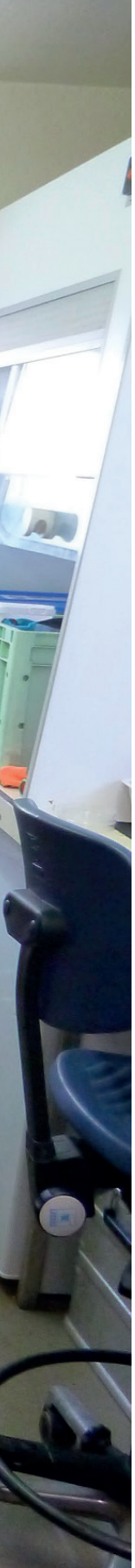


Figure 3: Graphical overview of the thesis. **Chapter 2** investigates the spatial distribution of small demersal fish using the Triple-D survey data. **Chapter 3** quantifies seasonal and species-specific energy densities of small demersal fish and combines these with the biomass data from Chapter 2 to create energy landscapes. In **Chapter 4**, species-specific primers are developed to distinguish *Ammodytes* species, represented by the coloured sandeels. **Chapter 5** investigates spatial habitat differences and diurnal behaviour of the two most abundant *Ammodytes* species using data from the WOT shellfish surveys in the Dutch coastal zone (indicated by the blue polygon).





2

Small fish biomass in the North Sea is far greater than previously estimated

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ABSTRACT

Small fish, including species with small adult sizes and juveniles of larger species, play a central role in marine food webs as prey for top predators, such as seabirds, marine mammals, and piscivorous fish. However, reliable data on small fish are lacking as conventional fisheries surveys primarily focus on larger, commercially important species and underestimate small fish. Consequently, little is known about the absolute biomasses and fine-scale distribution patterns of this important trophic group. Based on 1,307 quantitative Triple-D samples from the Dutch EEZ and the UK sector of the Dogger Bank, biomass densities were estimated for pooled small demersal fish and for the most abundant species individually. Our estimates suggest that small demersal fish biomass is at least twice as high as reported in trawl-based studies. Uniformly distributed species such as dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*) contributed most to the overall small fish biomass, while sandeel (Ammodytidae) showed particularly high local densities. These new prey biomass estimates might change our understanding of the North Sea ecosystem's carrying capacity, and establish a baseline for monitoring changes in small fish communities driven by climate change and human impacts.

1. INTRODUCTION

In marine food webs, small fish, which are defined as fish smaller than 30 cm (Rogers & Ellis, 2000; Daan et al., 2005), serve as a major prey source to (top) predators, such as piscivorous fish, seabirds, and marine mammals, by transferring energy from lower to higher trophic levels (Engelhard et al., 2014; Leopold, 2015; Aarts et al., 2019). The distribution and abundance of these small fish, which include small-bodied species and juveniles of larger species, play a crucial role in marine ecosystem functioning. Usually, the geographical distribution of prey species is one of the main drivers of predators' distribution and their foraging behaviour (Fauchald 2009; Sveegaard et al., 2012). Furthermore, prey availability is an important component for the carrying capacity of predator abundance in a bottom-up driven ecosystem. Estimating carrying capacity, as well as evaluating predation pressure and the potential impacts of fishing activities, requires absolute abundance estimations of prey (Fraser et al., 2007; Walker et al., 2017). However, conventional fisheries surveys that currently inform most marine management are primarily designed to collect annual comparable data on the distribution, abundance (stock size), and biological parameters of fish species of commercial importance (ICES, 2022). Even for these commercial species, (offshore) surveys are often not designed to quantify their early life stages. Hence, reliable absolute abundance estimates or distribution patterns of small fish are largely missing, despite the crucial ecological role they play.

The fish community in the North Sea has changed over the 20th and early 21st centuries, with a shift towards pelagic species and smaller body sizes (Rijnsdorp et al., 1996; Rogers & Ellis, 2000; Daan et al., 2005; Engelhard et al., 2011). This shift is partly explained by rising water temperatures due to climate change (Mackenzie & Schiedek 2007), which favours warm-water species that, on average, tend to have smaller body sizes (Hiddink & ter Hofstede 2008; Daufresne et al., 2009; ter Hofstede & Rijnsdorp 2011). The increase in small fish abundance is also associated with density-dependent processes resulting from reduced predation and/or competition, due to the selective removal of large predatory fish by fisheries (Daan et al., 2005). Furthermore, evidence suggests that maximum lengths within species were reduced by increased water temperatures and the effects of fisheries (Rijnsdorp 1993; Baudron et al., 2014). As a result, the relatively small herring (*Clupea harengus)*, sprat (*Sprattus sprattus)*, and Norway pout (*Trisopterus esmarkii)* are currently the most abundant pelagic fish species in the North Sea (Engelhard et al., 2014; Heessen et al., 2015). Scaldfish (*Arnoglossus laterna)*, solenette (*Buglossidium luteum)*, dragonet (Callionymidae), and various goby (Gobiidae) species are some of the most common small-bodied demersal species found in the North Sea (Callaway et al., 2002; van

Hal et al., 2010; Sell & Kröncke, 2013). Also, juvenile individuals of species that grow to larger sizes, such as sole (*Solea solea*), plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*), are common throughout the area (Bolle et al., 1994; Reiss et al., 2010; Heessen et al., 2015). Lastly, sandeel (Ammodytidae), which can be classified as both pelagic and demersal, are probably the most abundant small fish species in the North Sea (Engelhard et al., 2014). Their highly localized abundance, along with their presence both in the sediment and the water column, makes them a crucial food source for both pelagic and demersal predators (Jansen et al., 2013; Engelhard et al., 2014; Leopold, 2015; Aarts et al., 2019; Wilson & Hammond 2019). In this study we concentrate on the community of small demersal fish, including buried sandeel.

Various annual surveys take place in the North Sea to monitor demersal fish populations, but these sample small fish less effectively (Knijn et al., 1993). For example, the GOV trawl (Grande Overture Verticale with a 20 mm stretched mesh cod end) used in the International Bottom Trawl Surveys (IBTS) has relatively loose contact with the seabed, resulting in underrepresentation of species tightly associated with the sea floor, such as solenette, goby and dragonet (ICES, 2004). The other main demersal offshore survey, the Beam Trawl Survey (BTS), is equipped with a large beam (7 or 8 m) trawl that can effectively capture fish in or on top of the seabed due to tickler chains that penetrate and disturb the top layer. But a relatively large mesh size is used (40 mm stretched mesh cod end), which makes it inefficient for the sampling of small fish, such as gobies and solenette (ICES, 2004; Walker et al., 2017). The Demersal Fish Survey (DFS), carried out in the inshore waters of the Netherlands, Germany, and Denmark, is equipped with a smaller beam (3 or 6 m) and a finer mesh size (20 mm stretched mesh). It catches small species more efficiently, but despite higher catch efficiency for small fish, fish caught in the fishing path remains low: 10-40% (Aarts et al., 2019). Furthermore, the spatial coverage of the DFS is limited to the coastal areas with maximum depths of 25 m and, therefore, does not provide information about the small fish community for the more offshore and deeper parts of the North Sea.

Among gear types used in surveys in the North Sea, the 2 m beam trawl, set with a very fine mesh size (4 mm), is regarded as a more efficient gear to sample the smallest fish species, like gobies (Callaway et al., 2002; ICES, 2004; Reiss et al., 2006; Sell & Kröncke, 2013). However, as it is not used in standardized sampling programs, the 2 m beam trawl data lacks spatial and/or temporal resolution. None of the surveys mentioned above is regarded as adequate at effectively sampling sandeel – which is a clear data gap given the importance of sandeel in the food web. Sandeel are particularly difficult to sample due to their burrowing

behaviour and slender body shape (Knijn et al., 1993; ICES, 2004). For this species, acoustic methods are also subject to abundance uncertainties due to the fact that in spring and summer a variable proportion of sandeel are burrowed in the sediment while others forage in the water column (Freeman et al., 2004). Grab sampling during the winter, when sandeel are in the sediment, is considered as the only technique to quantitatively sample sandeel abundance (Mackinson et al., 2005; Johnsen & Harbitz 2013); however, due to the small sampling area (0.096 m^2) and patchy distribution of sandeel, many grab samples result in zero counts, even in areas where sandeel are present (Holland et al., 2005).

Thus, there is a lack of reliable data on (fine-scale) spatial and temporal patterns in the small demersal fish community, including (burrowed) sandeel. This leads to significant uncertainties in absolute prey estimates and, as a result, insights into the carrying capacity of the North Sea (Aarts et al., 2019; Ransijn et al., 2019). Furthermore, the lack of fine-scale prey distribution data complicates the understanding of predator foraging behaviour in seabird species (van Bemmelen et al., 2021; Fijn et al., 2022), and marine mammals, including harbour seal (*Phoca vitulina,* Aarts et al., 2016) and harbour porpoise (*Phocoena phocoena,* Haelters et al., 2011; Gilles et al., 2016). Those data uncertainties make it difficult to fully comprehend the role of small demersal fish in the functioning of the North Sea marine ecosystem.

This study was conducted to improve our understanding of the spatial distributions and absolute biomass of small benthic fish species in the southern North Sea, but mainly the Dutch Exclusive Economic Zone (EEZ). To that purpose the NIOZ Triple-D (deep digging dredge) was used. The Triple-D, which was originally designed to sample macrobenthic infauna and epifauna (Bergman & van Santbrink, 1994). The gear has a small mesh size (7×7 mm) and captures organisms within a range of 20 cm above and below the sea floor. The catch includes small bottom fish such as gobies and burrowed sandeel, but also juvenile flatfish. In this paper, a biomass distribution map of the pooled small demersal fish is presented. Those estimates are compared with existing estimates obtained with other gear types. Furthermore, species-specific distribution estimates are provided of the seven most abundant species in the Triple-D catches.

2. METHODS

2.1. Study area

The study area encompasses the Dutch Exclusive Economic Zone (EEZ) and the northwestern part of the Dogger Bank in the UK EEZ. The Dutch EEZ is characterized by its shallow nature, with depths generally less than 50 meters. The seabed predominantly consists of sandy substrates, except for the area around the Oyster Grounds, which consists of fine sand with up to 20% mud (Creutzberg et al., 1984). The coastal area receives a substantial influx of nutrients from river inflows and is characterized by high rates of primary production and secondary production by zooplankton, mesoplankton and macro-zoobenthic species (Duineveld et al., 1991; Prins et al., 2012). In the shallow parts (<30 m) the water column is mixed, while in deeper areas seasonal stratification may occur, accompanied by the formation of hydrographic fronts (Holt & Umlauf 2008; van Leeuwen et al., 2015).

2.2. Sampling gear, treatment, and design

The Triple-D ('Deep Digging Dredge') developed by the Netherlands Institute of Sea Research (NIOZ) (Bergman & van Santbrink, 1994) was used to collect the small fish data. This gear, which has a 7x7 mm mesh size, is rigged with a 20 cm wide cutting blade that penetrates 20 cm into the seafloor, a setup that also enables the sampling of burrowed sandeel. Furthermore, the design also enables catching fish up to 20 cm above the seabed. The sampling speed is 3 knots, and a measuring wheel enables precise estimation of the sampled surface area. Haul lengths were usually either 50 or 100 m, resulting in a sampling area of 10 or 20 m^2. See Witbaard et al. (2013) for more technical details of the Triple-D design and the hauling process.

On board, all fish from a catch were identified to species level, or to the species group for challenging species like goby (Gobiidae) or sandeel (Ammodytidae). Fish were measured down to the nearest 0.5 cm, and their wet weight was determined to the nearest 0.5 g using a marine scale (a Marel 2000). If a species was caught in high numbers, the total weights of all individuals within the same length class were recorded. For very large catches of a given species, a subsample was measured for length and weight, while the remaining fish were only counted. In cases of an excessively large total catch, subsampling was applied to the entire catch, and a sorting fraction was noted. Some of the data, particularly from the early years, consisted only of count information and mostly involved gobies. Lengths of damaged fish, aside from the occasionally high numbers of half cut sandeel, were reconstructed based on morphometric relationships.

Between 2006 and 2023 a total of 1307 locations were sampled, as illustrated in Fig. 1. The dataset includes data collected specifically for this study, along with older data obtained during research cruises in preceding years (see Fig. S1 and Witbaard et al., 2013). As a result, the survey design lacks a regular spatial and temporal scale, leading to variations in sample density across different areas and years. Sampling primarily occurred in the winter and early spring. A minority of samples was collected in June and October (see Fig. S2). Sampling was conducted aboard the RV *Pelagia* of NIOZ or the *Arca* of Rijkswaterstaat (North Sea Directorate).

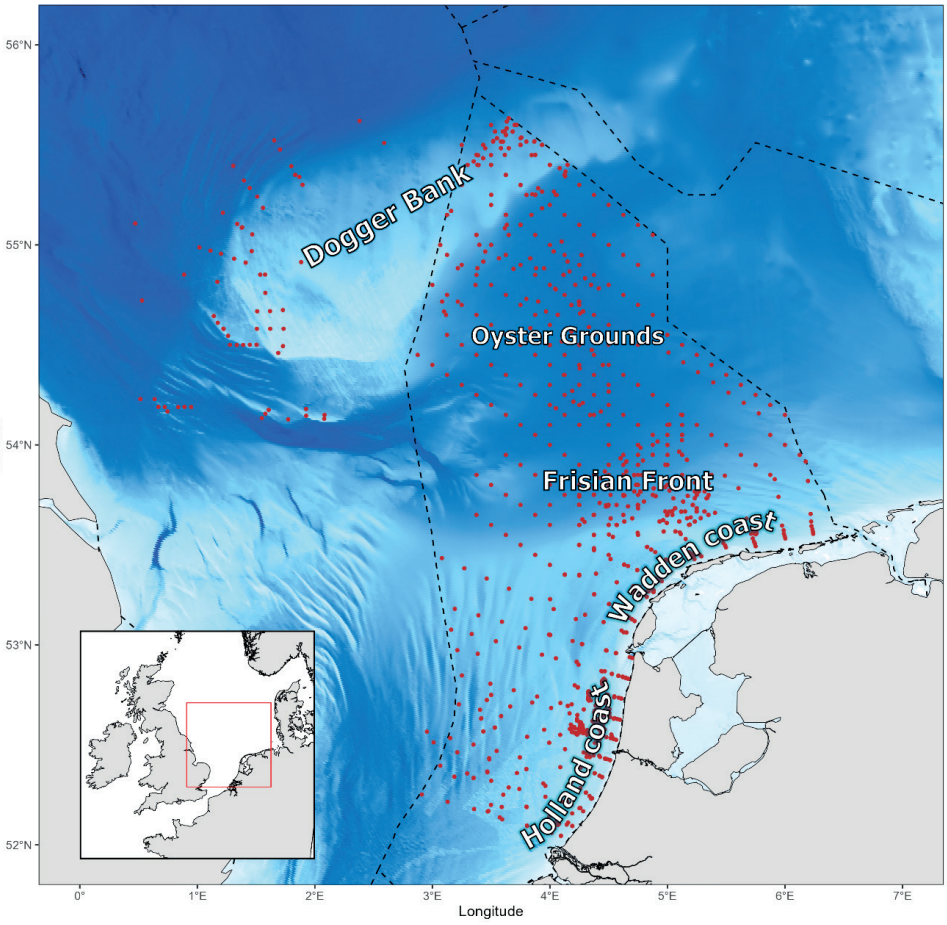


Figure 1: Triple-D sample locations, including bathymetry in the southern North Sea. The dashed line shows the border of the Exclusive Economic Zones of the Netherlands, UK, Germany, and Denmark.

2.3. Data processing

The quality of the fish data was checked for discrepancies in sizes and weights. The records in which either weight or length was missing were reconstructed using length-weight relationships. These relationships per species were established by fitting a linear regression through the log-transformed weight and length data from our own dataset. In those cases where Triple-D data were insufficiently available for a specific species (<10 entries), length-weight relationships from FishBase were used (Froese & Pauly, 2023). The length distribution of the measured subsample was used to predict the lengths of the remaining unmeasured but counted individuals. If no length distribution was available within the same haul, the length distribution of the same species from that corresponding survey was used for prediction. The length-weight relationships were then used to predict wet weights based on predicted lengths. Prior to the distribution analysis, all fish larger than 30 cm were removed from the dataset. The 30 cm threshold between "large" and "small" fish was used in compliance with Rogers & Ellis (2000) and Daan et al. (2005). However, because of their elongated and slender body types, pipefish Syngnathinae, hagfish (*Myxine glutinosa)*, and great sandeel (*Hyperoplus lanceolatus*) larger than 30 cm were kept in the dataset.

2.4. Environmental variables

Depth data (EMODnet), with a resolution of 1 by 1 km, and mud content percentage, with a resolution of 1 × 1 nautical miles (Bockelmann et al., 2018), were retrieved. For all sampling locations, depth and mud content were determined, based on the nearest data point from the depth and mud datasets. Depth at sampling locations ranged from 9 to 83 m, with most locations between 15 and 50 m deep (see Fig. S3). Mud content at sampling locations ranged from 0 to 36%, although the majority had less than 5% mud content (see Fig. S3).

2.5. Spatial analysis bottom fish distribution

A distribution map of small demersal fish was created by fitting a spatial latent-field model using Stochastic Partial Differential Equations (SPDE) within R-INLA (Integrated Nested Laplace Approximation) package (Rue et al., 2009; Zuur et al., 2017). The total fish biomass, all small fish species pooled together, per station was defined as the response variable in the following model:

$$\mathrm{F}_i \sim \mathrm{NB}(\mu_i) \tag{1}$$

$$\mathrm{E}(\mathrm{F}_i) = \mu_i \text{ and } \mathrm{var}(\mathrm{F}_i) = \mu_i + \frac{\mu_i 2}{k} \tag{2}$$

$$\log(\mu_i) = \beta_1 + \mathrm{offset}(\log\left(\frac{\text{distance}}{\text{fraction}}\right)) + \text{survey} + \mathrm{RW}(\mathrm{DOY}, \text{depth}, \text{mud content}) + u_i \tag{3}$$

The response variable F_i, which represented the fish biomass at position i, was assumed to follow a negative binomial distribution with the dispersion parameter *k*. β_1 is the intercept and log(haul distance/fraction) was included as an offset term to take into account different haul lengths and subsampling fractions. Survey effect was included as a random variable to capture annual variation and other potential survey variances. Seasonal trends in biomass were included by using a Day of Year (DOY) random walk (RW) smoother, starting from October 1st to ensure a continuous smoothing between December and January. This starting point was also chosen due to the sampling gap between June and October, making October 1st a more logical starting point (Fig. S2). Random walk trends were also used to identify biomass trends in relation to depth and mud content. Spatial biomass variance which could not be explained by survey effect, DOY, depth, or mud, was captured by a spatial latent field, represented by u_i. This spatial latent field captures (residual) spatial autocorrelation, described by a Matérn correlation function which is estimated by using Stochastic Partial Differential Equations (SPDE) (Rue et al., 2009, Lindgren et al., 2011, Zuur et al., 2017). INLA requires a mesh (see Fig. S4) consisting of triangles to determine the spatial autocorrelation.

A grid of 1 km² cells was created in the areas of interest (UK Dogger Bank and Dutch EEZ). For each grid cell, the median biomass as well as the 0.025 and 0.975 quantiles were calculated To estimate the average biomasses (and its 95% credible intervals) of the two areas of interest, we calculated the mean for both areas by taking the median and percentile values from all respective grid cells. Grid cells with depth or mud content outside the range of sampled locations were assigned values based on the nearest observed limits. For instance, the deepest sampled location was 83 m, all grid cells exceeding this depth were assigned the biomass estimate for 83 m. In the Dutch EEZ the spatial biomass predictions were made using survey "2019Feb_187" and Day of Year (DOY) = 143 as baselines. Survey "2019Feb_187" was chosen as this survey had relatively recent sampling and an extensive spatial coverage. DOY = 143 was selected because it corresponded to the day with the highest number of samples over all cruises (Fig. S2). At the UK Dogger Bank, only one survey was conducted, in June. Since no data was collected during winter, we did not produce winter predictions for this area. Instead, biomass predictions for the UK Dogger Bank were based on June conditions, using '2023Jun_65' and DOY = 265 as survey and seasonal baselines. Model validation involved simulating data from the posterior parameter estimates and comparing the simulated results to the observed data. Additionally, residuals were examined per explanatory variable and across spatial scales to identify potential patterns or anomalies (Zuur et al., 2017). For

the species-specific biomass predictions, the same approach as described above was applied, but with species-specific biomass as the response variable.

3. RESULTS

A total of 37 species (or species groups) were caught across the 1307 collected samples (Table S1). The most common taxa, ranked by their occurrence based on weight, were sandeels, dab, plaice, solenette, gobies, dragonet and scaldfish (see also Fig. S5). The species-specific length distributions for these seven most common species show that the Triple-D gear seldomly captured fish larger than 25 cm, but it was able to capture very small fish as small as 2-3 cm (Fig. 2). For some species, such as dragonet, plaice and dab, the length distributions are multimodal, which does not necessarily imply multiple cohorts as samples were collected in different years and over different seasons.

The observed median biomass density across all sampling locations, for all small bottom fish species combined, was 10.3 g m^{-2} (after correction for haul distance and sorting fraction; see Fig. S6). This pooled biomass density of small fish differed markedly across the sampling locations. At 90% of the sampling locations, the biomass density ranged from 1.5 to 39.2 g m^{-2} (see Fig. S6). However, at seven sampling locations, the biomass densities even exceeded 100 g m^{-2}.

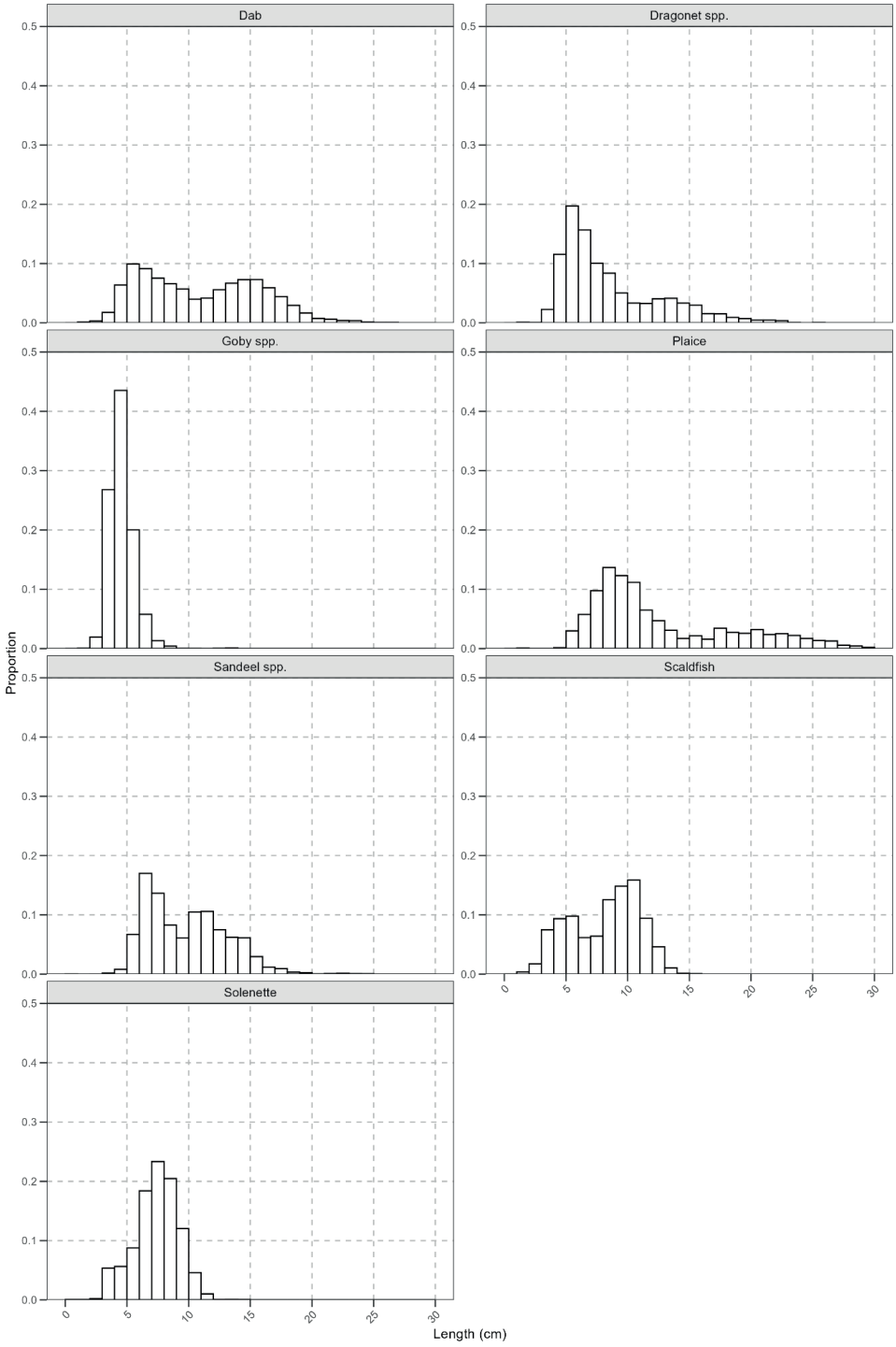


Figure 2: Observed length distributions of the seven most abundant (based on wet biomass contribution) small fish species sampled with the Triple-D.

3.1. Total small fish biomass distribution

In the Dutch EEZ, the predicted median small fish biomass for the winter period was estimated to be 10.8 g m^{-2}, while in the UK Dogger Bank, assessed during summer, the median biomass was 30.5 g m^{-2} (Table 1). Biomass was heterogeneously distributed, with local 'hotspots' of high biomass densities and broader areas where densities were considerably lower (Fig. 3). In the Dutch EEZ, high biomass densities, reaching up to 30 g m^{-2}, were predicted along the North Sea coast of the Wadden Islands and in the southern Dutch part of the Dogger Bank. Particularly low (<10 g m^{-2}) biomass areas were the southern Oyster Grounds, the shallow parts of the Holland coast, and the north and eastern part of the Dutch section of the Dogger Bank. The high average biomass for the UK Dogger Bank was largely driven by sampling locations near the 40 m depth contour. One region showed exceptionally high densities, exceeding 75 g m^{-2}. In contrast, the deeper off-bank areas to the north and west exhibited relatively low (<20 g m^{-2}) biomasses. At the central, shallow parts of the UK Dogger Bank, more moderate (20 - 35 g m^{-2}) densities were predicted.

In the model, depth explained part of the biomass, with lower biomass observed at depths below 20 m and peak biomass around 50 m (Fig. S7). Similarly, Day of Year (DOY) captured a seasonal biomass trend, with high biomass values in early autumn and lower biomass values in late winter (Fig. S7). In contrast, mud percentage did not account for any clear patterns in biomass distribution (Fig. S7). Survey effect appeared to be largely unimportant (Table S2). This suggests that most of the biomass variation between surveys was already captured by other variables (including the latent field).

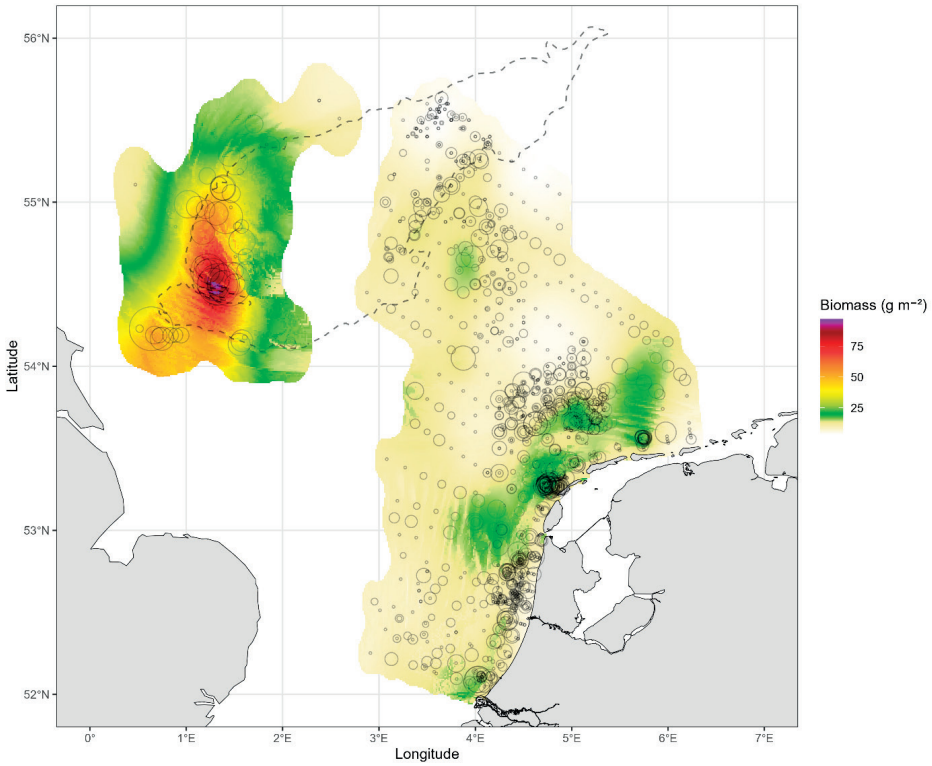


Figure 3: Distribution of total small fish (<30 cm) biomass in the southern North Sea. Biomass estimates for the Dutch EEZ are a winter prediction, while estimates for the UK Dogger Bank reflect summer conditions. Size of black circles correspond with the observed biomass densities per station (corrected for haul distance and sorting fraction). The 40 m depth contour of the Dogger Bank is indicated by the black dashed line.

3.2. Species-specific biomass distributions

The seven most abundant small fish taxa in the study area differed largely in abundance and spatial distributions (Fig. 4, Table 1). Plaice and dab were relatively homogeneously distributed across the entire study area, with relative high biomass densities ranging from 1 to 4 g m^{-2} in the Dutch EEZ and up to 8 g m^{-2} in at the UK Dogger Bank. The other species showed a more heterogeneous distribution. Sandeel, in particular, stood out with very high localized densities and large areas where it was entirely absent. For example, in the northwestern part of the UK Dogger Bank, sandeel biomass often exceeded 50 g m^{-2}. In contrast, the deeper parts of the UK Dogger Bank sandeel have not been found. In the Dutch EEZ, relatively high densities, up to 10 g m^{-2}, were predicted near Vlieland. However, sandeel also showed the largest areas of absence among the seven most abundant species, particularly on the Oyster Grounds and the Frisian Front. Dragonet was also heterogeneously distributed but had much lower densities than sandeel, with hotspot areas at the UK Dogger Bank and in

the Dutch coastal regions. In contrast, dragonet was rarely found within 20 km of the Dutch coast or in the northern part of the Dutch EEZ. Notably, scaldfish and solenette were also almost absent from that nearshore part of the Holland coast. Additionally, scaldfish was the only species with its highest densities on the Oyster Grounds, reaching up to 5 g m^2. High densities of solenette could be found at the central parts of the Dogger Bank. Gobies were mainly found in the coastal areas, at densities ranging between 2 and 4 g m^{-2}. Further offshore, including the UK Dogger Bank, goby densities were very low (< 0.5 g m^{-2}). Lastly, the pooled remaining species, with whiting, common sole and lemon sole as the main contributors (Table S1), were also quite uniformly distributed, with densities ranging between 1 and 6 g m^{-2}.

Figure S9 shows the biomass variance trends per species for each explanatory variable. DOY was an important factor for all species, although no consistent trend between the species can be observed. Depth was important for most species, except for plaice and the remaining pooled fish group. Shallow depths were for most species negatively associated with biomass. The exception was sandeel with relatively high biomass at shallow depths. Also mud content appeared to be an important factor for sandeel, which had clear preferences for bottoms with very low (< 5%) mud content. Gobies were the only other species group for which mud content explained part of the biomass variance, with preferred mud levels between 5 and 10%.

The mean biomass densities per area of interest (Table 1) shows that the uniform distributed species, plaice and dab, along with the pooled remaining fish contributed most to the overall fish. However, the extremely high sandeel densities at the UK Dogger Bank resulted in that sandeel accounted for the largest share of the biomass at the UK Dogger Bank.

Table 1: Predicted average biomass densities of small fish species by area. Biomass estimates for the Dutch EEZ are a winter prediction, while estimates for the UK Dogger Bank reflect summer conditions. The relative contribution to total fish biomass density is indicated in brackets. Please note that the relative contributions may not sum to exactly 100% due to the individual models used for each species.

	Biomass (g m^{-2})			
Taxa	**Dutch EEZ**	**q0.025 - q0.975**	**UK Dogger Bank**	**q0.025 - q0.975**
All combined	10.8	6.6 - 18.0	30.5	14.8 - 63.7
Dab	2.1 [19.4%]	1.0 - 4.8	3.1 [10.2%]	0.9 - 12.6
Dragonet spp.	0.4 [3.7%]	0.1 - 2.0	0.8 [2.6%]	0.1 - 10.8
Goby spp.	0.5 [4.6%]	0.2 - 1.3	0.1 [0.3%]	0.0 - 0.4
Plaice	1.3 [12.1%]	0.5 - 3.5	3.7 [12.1%]	0.8 - 17.7
Sandeel spp.	0.5 [4.6%]	0.1 - 3.2	4.3 [14.1%]	0.4 - 86.5
Scaldfish	0.5 [4.6%]	0.2 - 1.3	0.6 [2.0%]	0.1 - 3.3
Solenette	0.8 [7.4%]	0.2 - 3.5	1.4 [4.6%]	0.1 - 19.2
Remaining	1.4 [12.9%]	0.6 - 3.0	4.4 [14.4%]	1.6 - 13.0

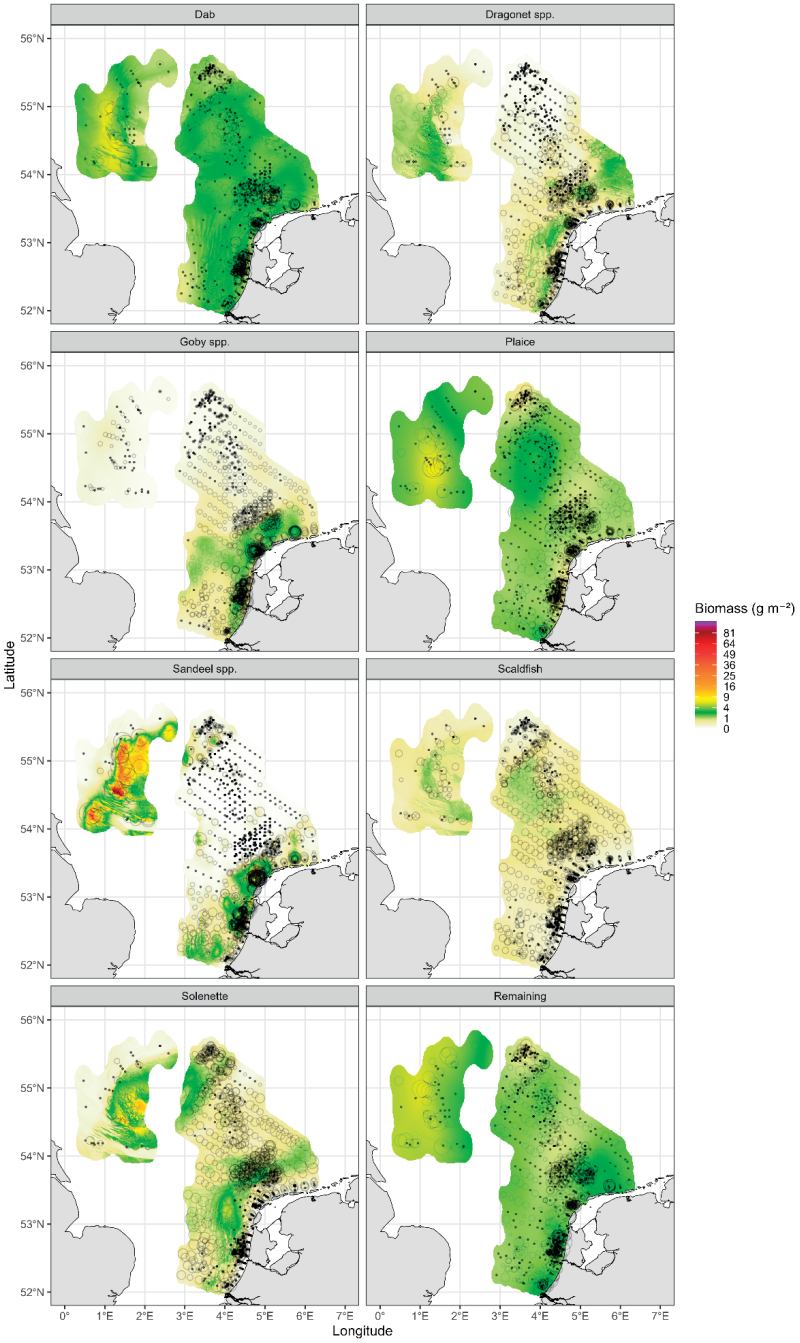


Figure 4: Distribution of biomass per small (<30 cm) fish species and all remaining small fish pooled in the southern North Sea. Biomass estimates for the Dutch EEZ are a winter prediction, while estimates for the UK Dogger Bank reflect summer conditions. Size of black circles correspond with the observed biomass densities per station (corrected for haul distance and sorting fraction). The 40 m depth contour of the Dogger Bank is indicated by the black dashed line.

4. DISCUSSION

4.1. Biomass density

This study provides new estimates on the biomass densities and spatial distributions of small demersal fish species for the southern North Sea, an area where these species are recognized as critical prey for a variety of (top) predator species. In the Dutch EEZ, the homogenous spread dab and plaice contributed most to the overall biomass of small fish. But sandeel contributed most at the UK Dogger Bank area, due to very high localized biomass densities.

The catch composition of the Triple-D appeared to be consistent with the composition of the fish community as sampled by the 2 m beam trawl (Callaway et al., 2002; Neumann et al., 2013; Sell & Kröncke, 2013). However, there was a large difference in average biomass of the two gear types. Sell & Kröncke (2013) observed, in spring, a biomass of 0.94 g m^{-2} on the Dogger Bank in 2006. Our June estimate is 30.5 g m^{-2} for the same area, which is significantly higher (Table 2). Sandeel contributed largely to this biomass (4.3 g m^{-2}), which is poorly sampled by the 2 m beam trawl, however the biomass difference when this sandeel biomass was subtracted (26.2 g m^{-2} versus 0.94 g m^{-2}) remains substantial. A temporal effect (2006 versus 2023) cannot be excluded but the large difference suggests that it is likely that the Triple-D is very effective in capturing small fish. This may be due to the Triple-D's fine mesh size, high towing speed, and its ability to catch fish buried in the sediment.

Several other studies have used data from the annual surveys to assess densities of fish biomass in the southern North Sea. For example, Greenstreet et al. (2007) used the IBTS summer data collected between 1998 to 2004. Their estimates for the Dutch EEZ, corrected for catchability and including all large fish over 30 cm, ranged from 0.7 to 6.0 g m^{-2} but with a peak to 8.5 g m^{-2} at the Dutch Dogger Bank. Sandeel was excluded, as it is poorly sampled by the IBTS gear. We arrived, with sandeel biomass subtracted, at a mean biomass density of 10.3 g m^{-2} for the Dutch EEZ in the winter period (Table 2). The IBTS estimate by Greenstreet et al. (2007) also includes fish >30 cm, while our estimate omits those size classes. This suggests that the IBTS underestimates the biomass of small bottom fish. Even after correcting for catchability of the IBTS gear. The underestimation of small fish biomass in the IBTS survey becomes even more pronounced when focusing on fish weighing between 8 and 31 g, being prey for piscivorous fish (Greenstreet et al., 2007). This weight range is roughly equivalent to flatfish between 10 and 15 cm total length. According to Greenstreet et al. (2007), the biomass density for this weight selection varied from 0.05 to 0.8 g m^{-2}. For fish meeting the same criteria but caught in the

Triple-D (see supplemental material; Fig. S10), we arrived at an estimate of 2.7 at the Dutch EEZ g m^{-2} (Table 2). This is almost 4 times higher than Greenstreet's estimate.

Aarts et al. (2019) estimated biomass density along the Dutch coast specifically for species identified as seal prey. They looked at bull-rout (*Myoxocephalus scorpius*), cod (*Gadus morhua*), common dragonet (*Callionymus lyra*), five-bearded rockling (*Ciliata mustela*), flounder (*Platichthys flesus*), whiting, dab and plaice. They found an average density of 2.5 g m^{-2} for the period from 1987 to 2016, based on BTS summer data. For the same selection of species, but caught with the Triple-D in winter, in the same geographic area, we found a biomass density of 6.1 g m^{-2} (Table 2; Fig. S11) which is more than two times higher. When all species, including important seal prey species such as goby and sandeel, were included, the biomass became 15.1 g m^{-2}. It is important to note that due to differences in mesh size, differences in length distributions, with larger individuals included in the BTS dataset, are likely.

On basis of the DFS survey in the near-coastal zone Aarts et al. (2019) also studied the biomass of seal fish prey, thereby including sandeel. The DFS is designed to better capture small (flat) fish, although catch efficiencies for sandeel are low. Again, differences with our results are substantial. Aarts et al. (2019) reported an average density of 0.6 g m^{-2} for the years 1970 to 2016, whereas our estimate of 7.0 g m^{-2} (sandeel included) or 4.0 g m^{-2} (without sandeel) was significantly higher (Table 2; Fig. S11). When considering all small fish caught in the Triple-D, we predict a small fish biomass of 11.1 g m^{-2} in the DFS survey area.

Table 2: Overview of fish biomass in the southern North Sea by gear type, compared with Triple-D estimates for the same geographical area. The Triple-D "Selection" column presents biomass estimates based on the same species selection as the respective gear type. The "sandeel excluded column" shows the triple-D estimate without sandeel. The Triple-D "All" column includes all small fish (<30 cm) caught by the Triple-D. An asterisk (*) indicates that sandeel were specifically excluded in the compared study. A double asterisk (**) denotes that the estimate refers to the UK Dogger Bank summer prediction.

								Triple-D biomass (g m^{-2})		
Area	**Gear/ survey**	**Catchability corrected**	**Sampling years**	**Sampling season**	**Study**	**Fish selection**	**Fish biomass (g m^{-2})**	**Selection**	**Sandeel excluded**	**All**
Dogger Bank	2 m beam	No	2006	April, May	Sell & Kröncke 2013	No	0.94	-	26.2**	30.5**
Southern North Sea	GOV/IBTS	Yes	1998-2004	July-October	Greenstreet et al., 2007	No*	0.7-6.0	-	10.3	10.8
Southern North Sea	GOV/IBTS	Yes	1998-2004	July-October	Greenstreet et al., 2007	8-31 g*	0.05-0.8	2.7	-	-
Netherlands northern coast	7 or 8 m beam/BTS	No	1987-2006	July-September	Aarts et al., 2019	Species selection*	2.5	6.1	-	15.1
Netherlands northern coast	6 m beam/ DFS	No	1987-2006	September, October	Aarts et al., 2019	Species selection	0.6	7.0	4.0	11.1

The comparisons of estimated fish density with the other sampling methods suggest that the catchability of the Triple-D is high. This makes it an effective sampling gear for small demersal fish. Even after correcting for catchability in the IBTS survey, the Triple-D still achieves a higher catch-rate for small fish. One of issues is that catchability correction factors for small fish are not reliable. The fundamental challenge in estimating catchability is the requirement to know the absolute biomass of a species. This is feasible for larger, commercially important species. For these species, cohorts can be tracked over time using catch data, allowing for accurate biomass estimates. In contrast, this approach is not applicable to small or juvenile fish, where such data is lacking, which makes accurate catchability estimates more difficult. Another issue is the inability to correct for false zero catches, i.e. where fish are present but not caught (e.g. because they are too small or buried in the seabed). Correction factors are essentially scaling adjustments (Fraser et al., 2007; Walker et al., 2017). Applying them to zero values would consequently remain recorded as zero. It is evident that dedicated gear types with high catchability are needed to accurately estimate small bottom fish biomass. Since small fish encompass a significant proportion of the total fish biomass, those small fish estimates are also needed to accurately determine the total fish biomass. Moreover, biomass estimates are much more sensitive to variations in catchability when the gear efficiency is exceedingly low. Consequently, the trends in fish abundance that are derived from the fish surveys may not only capture changes in fish abundance, but also changes in catchability due to changes in environmental conditions, such as turbidity and water temperature.

Because sampling years do not always overlap between our study and previous compared studies, the differences in biomass densities could reflect changes in abundance as observed in the 20th century (Daan et al., 2005; Engelhard et al., 2011; Rijnsdorp et al., 1996; Rogers & Ellis, 2000). In contrast to the Large Fish Index (Lynam & Piet, 2023), no equivalent indicator exists for small fish, making it difficult to assess whether the observed increase in small fish biomass during the 20th century has continued into the 21st century. However, some species-specific trends are available. Of the seven most abundant species in this study, scaldfish and solenette numbers have been continuously increasing in the North Sea (van Hal et al., 2010; CLO, 2023). Dragonet declined strongly since 2012 (CLO, 2023), but the remaining juvenile dab and plaice, sandeel and gobies have not shown clear upward or downward trends (Tulp et al., 2017; ICES, 2023a,b; ICES, 2024c; CLO, 2023). Given the lack of a clear increasing trend in abundance or biomass of small bottom fish across the sampling years of the compared studies, it is likely that the observed differences in biomass reflect

largely differences in gear catchability rather than an actual increase in the small fish community.

4.2. Distribution

Small demersal fish are particularly abundant in the southern North Sea (Callaway et al., 2002). In our study we observed a high fish biomass at the western Dogger Bank area, which was not identified by Callaway et al. (2002). This difference might be partly attributable to the large sandeel numbers caught in the Triple-D, which cannot be adequately sampled by a 2 m beam trawl, the gear used by Callaway et al. (2002). Callaway et al. (2002) neither identified strong spatial differences in abundance within Dutch EEZ, whereas the present study indicates that biomass distributions appear more heterogeneous. This disparity might be caused by the patchy distribution of sandeel (Engelhard et al., 2008; Tien et al., 2017), which contributes largely to the spatial patterns of small fish biomass.

We generated individual maps for the seven most abundant species. The distribution patterns of these species corresponded with the patterns based on the conventional IBTS and BTS survey data (Heessen et al., 2015). The coastal occurrence of dragonet and goby distribution is consistent with historical observations collected with dedicated beam trawls (Fonds 1973, van der Veer et al., 1990). The offshore distribution of small flatfish, including juvenile dab and plaice, supports the recent observations that small flatfish are moving northwards to more offshore areas (van Keeken et al., 2007; van Hal et al., 2010). For sandeel, commercial fisheries data are the primary source of information for their distribution in the North Sea (Jensen et al., 2011). Those observations are based on sandeel distribution during summer when sandeel are in the water column. The areas where we observed high densities overlap with the areas identified on basis of fisheries data, but at UK Dogger Bank also align with high sandeel densities based on sandeel specific studies (Engelhard et al., 2008; Langton et al., 2021). Closer to the Dutch coast, sandeel fishing effort is low, and sandeel dedicated studies have been limited to a study in the Voordelta area (Tien et al., 2017) and in the north, between the Wadden islands of Terschelling and Ameland (van Hal et al., 2021). As a result, information on sandeel distribution in these coastal waters remains sparse. This study therefore makes a significant contribution to filling the knowledge gap regarding sandeel distribution within the larger Dutch EEZ area. We did not relate our observed densities at the UK Dogger Bank with those sandeel specific studies, or with ICES sandeel stock assessments.

4.3. Limitations of the study

The Triple-D dataset is a composite which includes data from multiple surveys spread over the years and designed with different aims. Therefore, it does not cover a constant area and sampling period (Fig. S1). This is assumed to be less of a concern for a variety of benthic macro-invertebrates that comprised most of the original target organisms of the Triple-D sampling. For example, bivalves exhibit limited inter-annual and seasonal variations in abundance and distribution due to their sedentary lifestyle and long-life span. In contrast, several fish species are highly mobile and can display large annual population fluctuations (Shelton & Mangel, 2011), which are likely to lead to variations in their distribution and abundance. Seasonal migration also results in variations of distribution and biomass (Hunter et al., 2003). To account for those temporal dynamics, survey and the DOY effect were included as explanatory variables in the models. DOY proved to be an important variable in all models. In the all-small-fish model, DOY followed an ecologically expected pattern: biomass peaked in summer, declined through winter—likely due to mortality and limited growth—and then increased again as growth potentially outpaced mortality towards summer.

To better understand the temporal patterns, raw observations of the pooled small fish in those areas which were sampled multiple times (Fig. S12), were analysed. A maximum 1.6-fold difference in biomass was observed between years sampled in the same season (Fig. S13). This data comparison also showed that seasonal differences were more pronounced. For example, in the Vlieland area, the observed biomass in October 2019 nearly tripled compared to March 2021. In the Frisian Front highest biomass was found early autumn while in winter lower biomass was found. The Holland coast South was the only area sampled in both winter and summer, which showed a biomass difference of 150%. In general, these observed seasonal patterns align well with the DOY effect in the small fish model. In the species-specific models, DOY revealed a variety of patterns: most species showed increasing biomass toward summer, but gobies and dab decreased. These trends may reflect species-specific differences in growth, mortality or seasonal migration, which warrant further investigation. Such insights could be gained through multiple surveys conducted throughout the year in the same area.

Only one survey was conducted in the UK Dogger Bank area, with low density of sampling stations in the deeper parts. Consequently, the model outcomes have a relatively large uncertainty (Table 1). Additionally, the dab observations in the Dutch EEZ likely introduced a large autocorrelation distance in the model, which does not seem very applicable to dab observations in the deeper parts of the UK Dogger Bank area.

Our estimates might misrepresent total small fish biomass as hard-substrate areas were not included in the analysis. As is the case with most RV-based research surveys, the Triple-D cannot sample at locations with rocky substrates, shipwrecks, cables, pipelines, in wind farms, or around oil platforms. It is known that these three-dimensional more complex hard substrate areas attract fish, may host higher fish biomass, and in comparison to the surrounding soft sedimentary environments, different species and fish densities could inhabit those areas (Wright et al., 2020). Other studies are needed to account for those areas when estimating total small fish biomass.

4.4. Implications and applications

This study suggests that biomass of small bottom fish in the southern North Sea is substantially higher than estimated before on basis of the 2 m beam trawls, BTS, IBTS or DFS surveys. Consequently, studies examining prey-predator relationships and relying on these data may have underestimated prey abundance. For example, Aarts et al. (2019) may have overestimated the predation pressure exerted by harbour seals (*Phoca vitulina*) due to underestimated prey abundance, as discussed earlier. This underestimation is particularly relevant for species such as sandeel, which have low catchability in conventional annual survey fishing gears. Consequently, since prey availability is an important aspect of the carrying capacity, the revised estimates of prey availability may change our understanding of how many predators can be sustained in the southern North Sea.

The data suggest that the Triple-D has a higher and less variable catching efficiency for small demersal fish living in soft sediments biotopes when compared to the conventional trawling gears applied in fisheries surveys. Still, experimental studies (e.g. Reiss et al., 2006), or specific catchability analyses, similar to Fraser et al. (2007) or Walker et al. (2017), are needed to quantify the catchability of the Triple-D of the various small demersal fish species. For example, there is a risk that the shape of the dredge could create a surplus inflow due to current-induced suction caused by waterflow over the net. Future studies should attempt to estimate catchability for this gear type, e.g. by pair-wise comparison of measurements taken using other gear types, like box-cores or other dredge samples.

The high catchability of small fish suggests that more realistic estimates of the small demersal fish biomass can be obtained. Reliable estimates are needed to establish a baseline in prey availability, carrying capacity, and their implications for other trophic levels. This is particularly important in the perspective of anthropogenic influences and climate change currently impacting the North

Sea ecosystem. Accurate fish biomass estimates are also urgently needed in studies focusing on food web structure (Lynam et al., 2017; Stäbler et al., 2018) and assessment of fisheries pressure on the ecosystem (Shephard et al., 2015).

The maps presented here can help identify potential foraging areas for benthic predators in the southern North Sea. The overall biomass map may inform studies on generalist feeders like seals, while species-specific maps are more useful for specialists. There are large variations in the distribution patterns of the prey species, as seen in the species-specific distribution maps. For instance, the distributions of dab and plaice are rather homogeneous, whereas the distribution of sandeel is highly heterogeneous with well-defined density hotspots. Such a heterogeneous, but predictable distribution can be exploited by predator species, aligning with the principles of Optimal Foraging Theory (MacArthur & Pianka, 1966). By targeting specific areas with high prey densities, predators can maximize foraging efficiency, reducing the need to roam large areas where prey densities are lower. Prey species that show strong preference for specific habitat, such as sandeel (Holland et al., 2005; Langton et al., 2021; Tien et al., 2017), might provide a more predictable food source than more mobile prey species that show less specific habitat preferences.

Although the most abundant small fish species are not threatened, their key trophic role in marine food webs (Bulman et al., 2001; Cury et al., 2011; Pikitch et al., 2014; Flores-Ortega et al., 2020) makes accurate spatial information on their distribution essential for ecosystem-based management. This information can support marine spatial planning to identify suitable locations for e.g. wind farms, shipping lanes and marine protected areas. This is especially important for the North Sea and other regions where there is high demand by multiple users for the limited space available, but where spatial information on small demersal fish is limited due their under-representation in traditional surveys. We therefore recommend a wider adoption of surveys specifically designed to assess their biomass.

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SUPPLEMENTARY MATERIAL

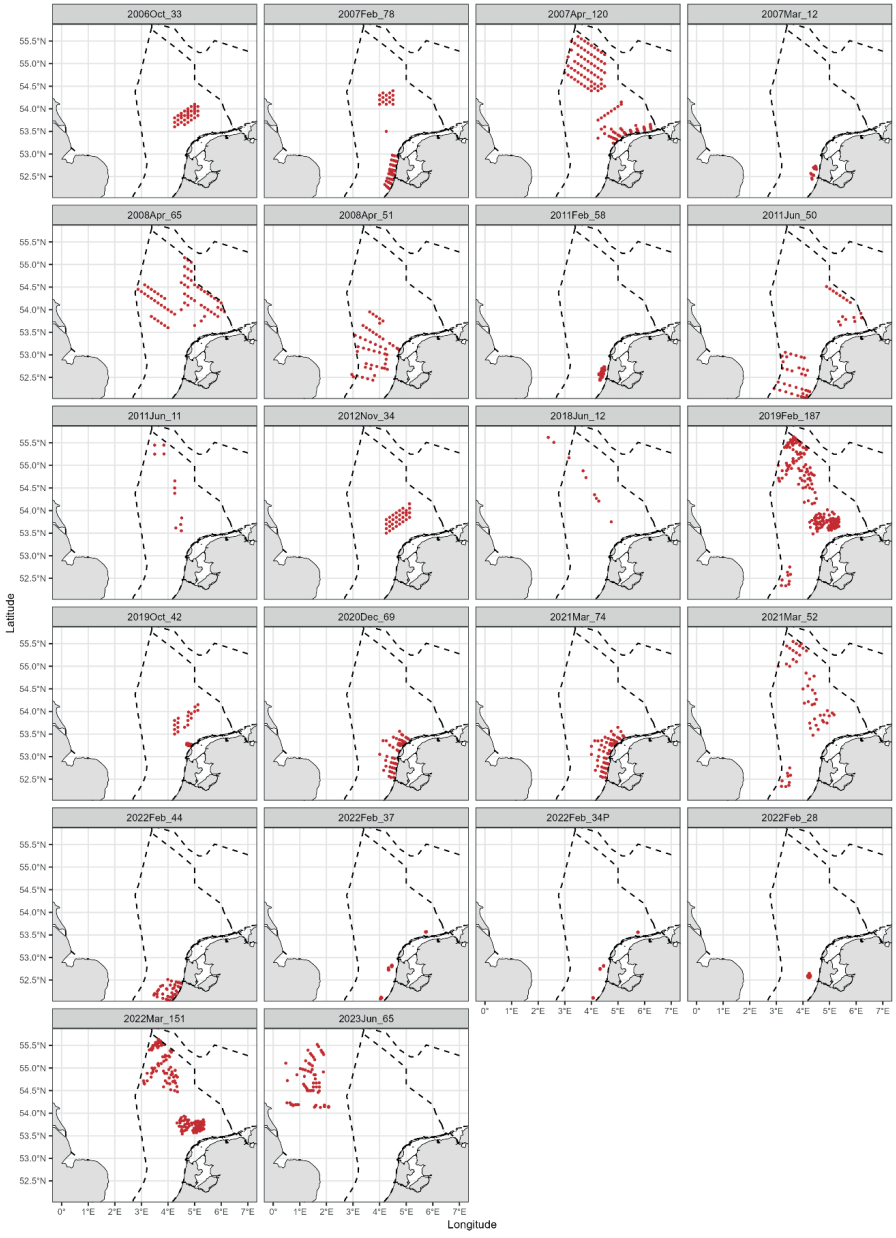


Figure S1: Spatial overview of Triple-D samples from each conducted survey. The survey name consists of year and month when survey was conducted, along with the number of samples taken during that survey. 2022Feb_37 and 2022_Feb34P, are sandpit samples (P) and the reference areas. The dashed lines indicated the Exclusive Economic Zones of the Netherlands, UK, Germany, and Denmark

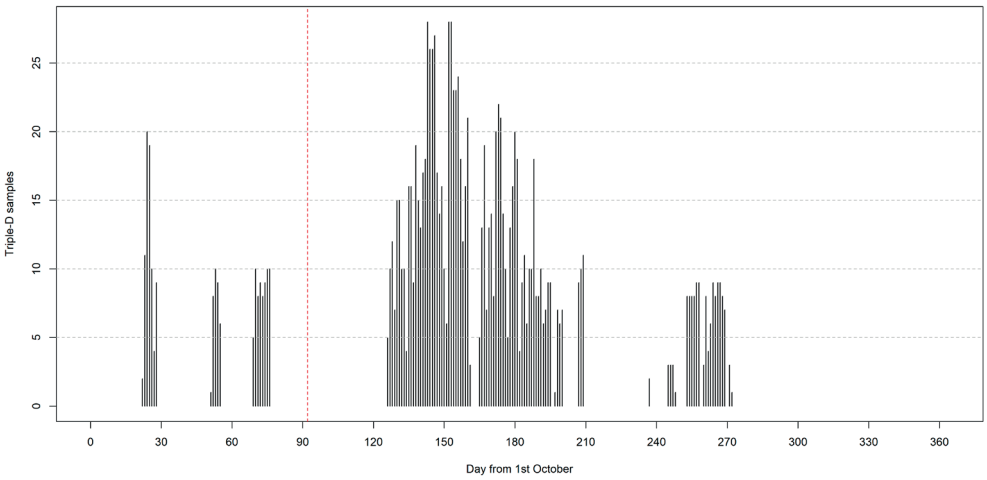


Figure S2: Number of Triple-D samples taken per day across all years. The day count starts from October 1st to ensure a smooth transition between December and February samples. The red vertical line indicates January 1st.

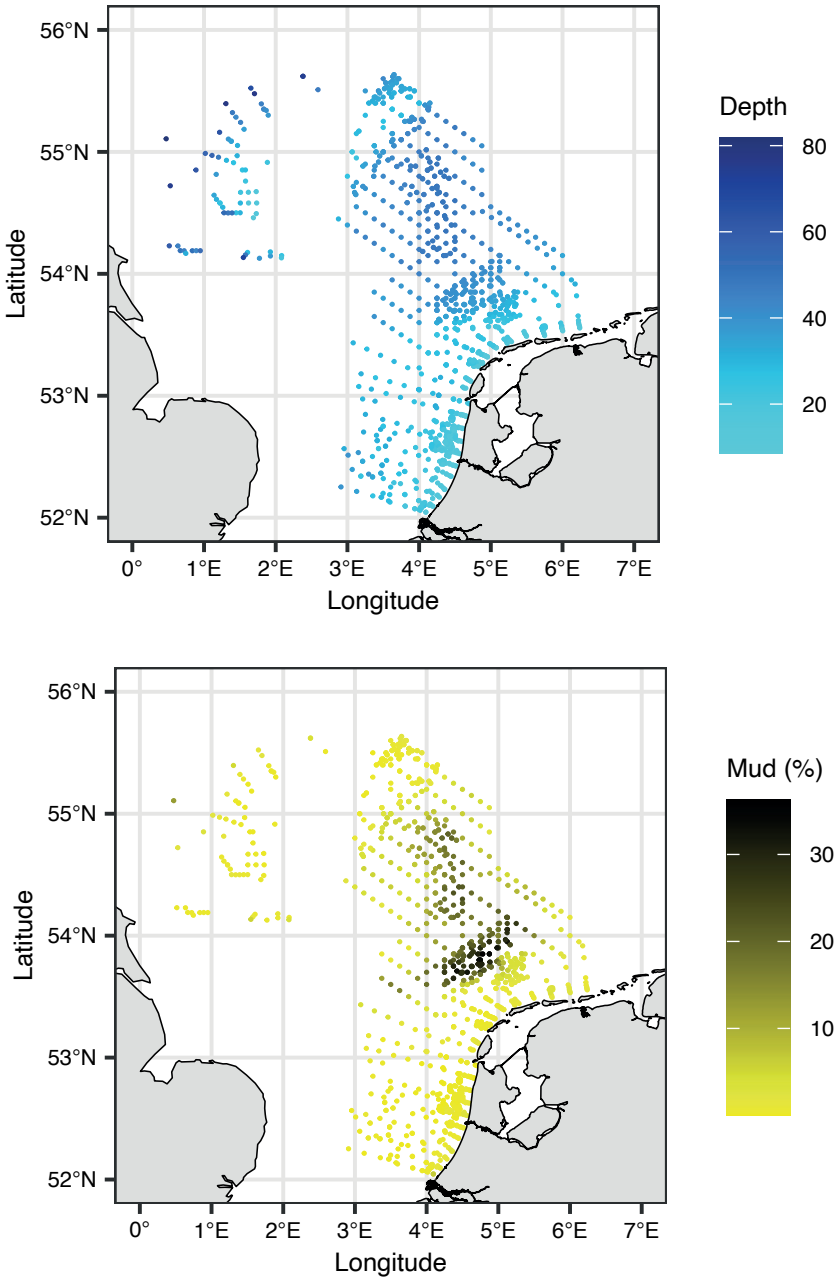


Figure S3: Depth, and mud content (%) at the 1307 Triple-D sampling locations.

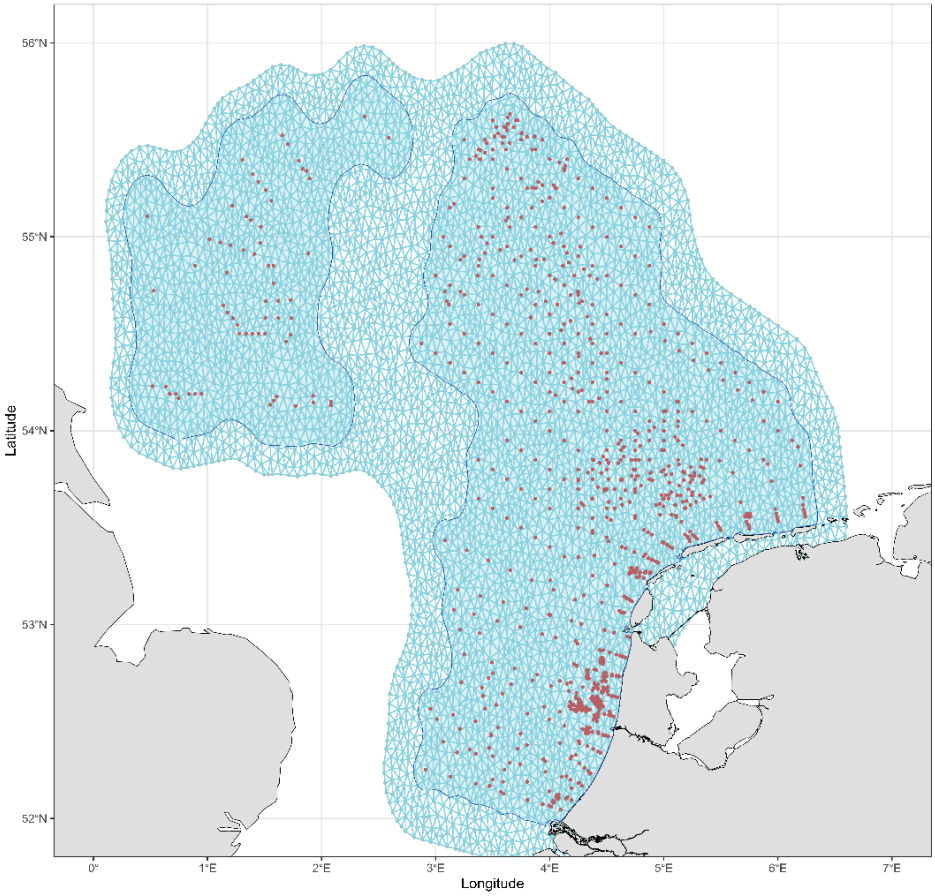


Figure S4: INLA mesh including Triple-D sampling locations (brown) and areas used for biomass predictions (within dark blue polygons).

Table S1: Small fish species (<30 cm) observed in the Triple-D catch. The contribution per species represents its fraction of the total observed wet biomass, adjusted for sorting fraction and haul distance.

Common name	Scientific name	Contribution (%)
Sandeel spp.	*Ammodytidae*	19.4
Common dab	*Limanda limanda*	17.2
European plaice	*Pleuronectes platessa*	15.4
Solenette	*Buglossidium luteum*	14.8
Goby spp.	*Gobiidae*	10.0
Dragonet spp.	*Callionymida*	5.3
Mediterranean scaldfish	*Arnoglossus laterna*	4.4
Whiting	*Merlangius merlangus*	4.1
Common sole	*Solea solea*	2.6
Lemon sole	*Microstomus kitt*	1.5
Rockling spp.	*Lotidae*	1.4
Cottidae spp.	*Cottidae*	0.6
Lesser weever	*Echiichthys vipera*	0.6
European flounder	*Platichthys flesus*	0.5
Gurnards spp.	*Triglidae*	0.5
Pipefish spp.	*Syngnathiformes*	0.4
Hooknose	*Agonus cataphractus*	0.3
Thorny skate	*Amblyraja radiata*	0.3
American plaice	*Hippoglossoides platessoides*	0.2
Thickback sole	*Microchirus variegatus*	0.1
Striped red mullet	*Mullus surmuletus*	0.1
Rock gunnel	*Pholis gunnellus*	0.1
Turbot	*Psetta maxima*	0.1
Gadiformes	*Gadiforme*	<0.1
Atlantic cod	*Gadus morhua*	<0.1
Short-snouted seahorse	*Hippocampus hippocampus*	<0.1
Megrim	*Lepidorhombus whiffiagonis*	<0.1
Common seasnail	*Liparis liparis*	<0.1
Atlantic hagfish	*Myxine glutinosa*	<0.1
Norwegian topknot	*Phrynorhombus norvegicus*	<0.1
Fish, unidentified	*Pisces*	<0.1
Flatfish, unidentified	*Pleuronectiformes*	<0.1
Skate spp.	*Raja*	<0.1
Brill	*Scophthalmus rhombus*	<0.1
Small-spotted catshark	*Scyliorhinus canicula*	<0.1
True soles spp.	*Soleidae*	<0.1
Weever fish spp.	*Trachinidae*	<0.1
Pouting	*Trisopterus luscus*	<0.1

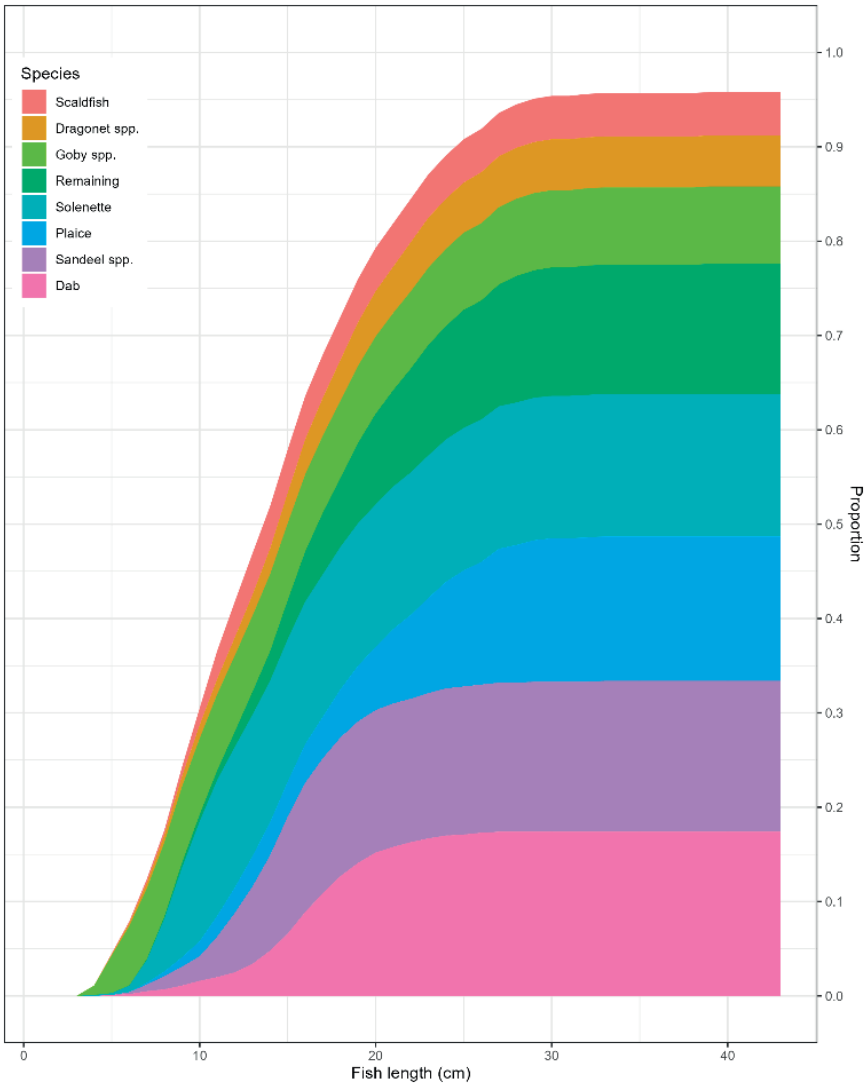


Figure S5: Cumulative biomass contribution of small fish (<30 cm) from the Triple-D catch, showing eight key small fish taxa and all other species combined. Fish lengths can exceed 30 cm due to species such as pipefish, hagfish, and great sandeel still being classified as small species despite their larger size. Additionally, some damaged fish could not be measured for length (mainly broken sandeel), causing the curve not to reach a proportion of 1.

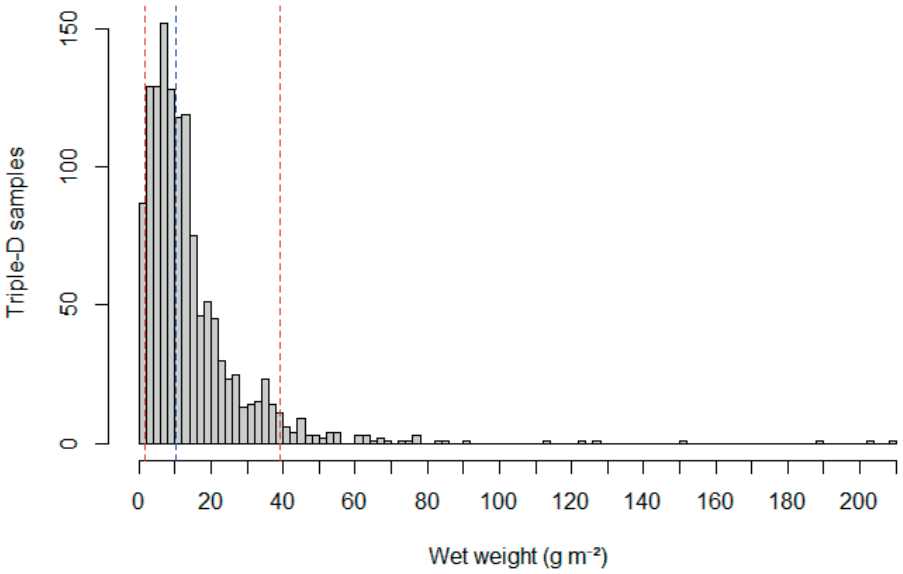


Figure S6: Biomass of small fish (<30 cm) observed across 1,307 Triple-D sampling locations, adjusted for sorting fraction and haul distance. The blue dashed line indicates the median biomass, while the red dashed lines mark the 0.05 and 0.95 quantiles.

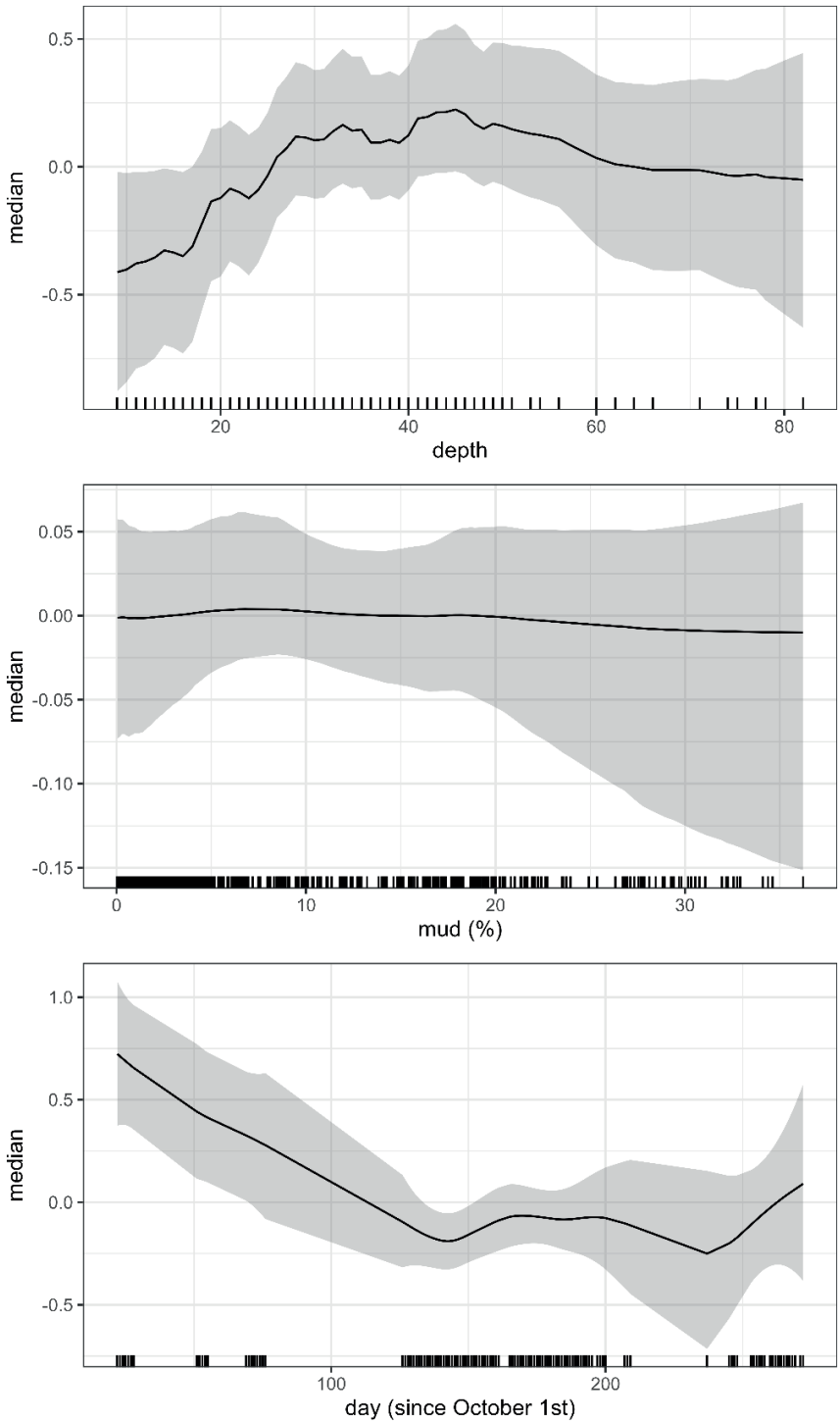


Figure S7: The marginal effect of depth, mud content, and Day of Year (DOY) for the biomass of the pooled small fish (<30 cm) with a 95% credible interval.

Table S2: Posterior survey effect, mean, standard deviation (SD) and 95% credible intervals for the survey effect in the small fish (<30 cm) model.

Survey name	mean	sd	0.025quant	0.975quant
2006Oct_33	0.01	0.15	-0.27	0.31
2007Apr_120	-0.16	0.10	-0.36	0.02
2007Feb_78	0.12	0.10	-0.07	0.33
2007Mar_12	0.06	0.14	-0.20	0.35
2008Apr_52	0.08	0.14	-0.18	0.38
2008Apr_65	0.06	0.12	-0.17	0.33
2011Feb_58	-0.13	0.12	-0.38	0.09
2011Jun_11	-0.11	0.17	-0.50	0.19
2011Jun_50	0.13	0.15	-0.14	0.46
2012Nov_34	-0.01	0.15	-0.31	0.28
2018Jun_22	-0.19	0.18	-0.62	0.10
2019Feb_187	0.11	0.09	-0.06	0.29
2019Oct_42	-0.01	0.14	-0.31	0.27
2020Dec_69	0.02	0.16	-0.30	0.34
2021Mar_52	0.04	0.11	-0.16	0.26
2021Mar_74	-0.13	0.11	-0.36	0.08
2022Feb_44	-0.10	0.12	-0.36	0.13
2022Feb_37	0.17	0.13	-0.06	0.44
2022Feb_34P	0.12	0.13	-0.10	0.40
2022Feb_28	-0.23	0.17	-0.61	0.04
2022Mar_151	0.02	0.10	-0.17	0.22
2023Jun_65	0.14	0.20	-0.19	0.61

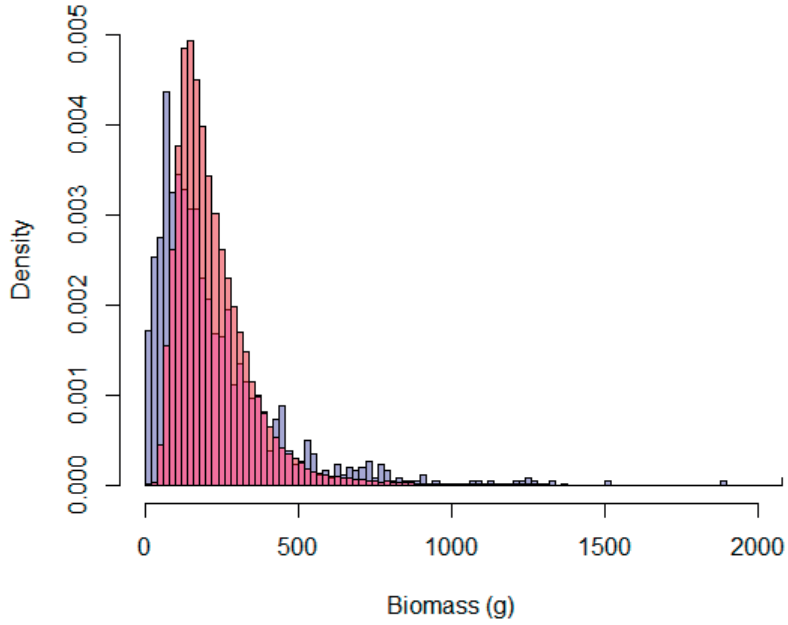


Figure S8: Observed, uncorrected for haul distance or sorting fraction, small fish biomass (blue) and simulated (100x) results based on the posterior parameters (red) of the fitted model. The discrepancy arises because the model applies spatial smoothing, leading to higher predicted values for sampling locations which are surrounded by locations with higher biomasses. The opposite is also true for locations with relative high biomass values than neighbouring locations with lower values.

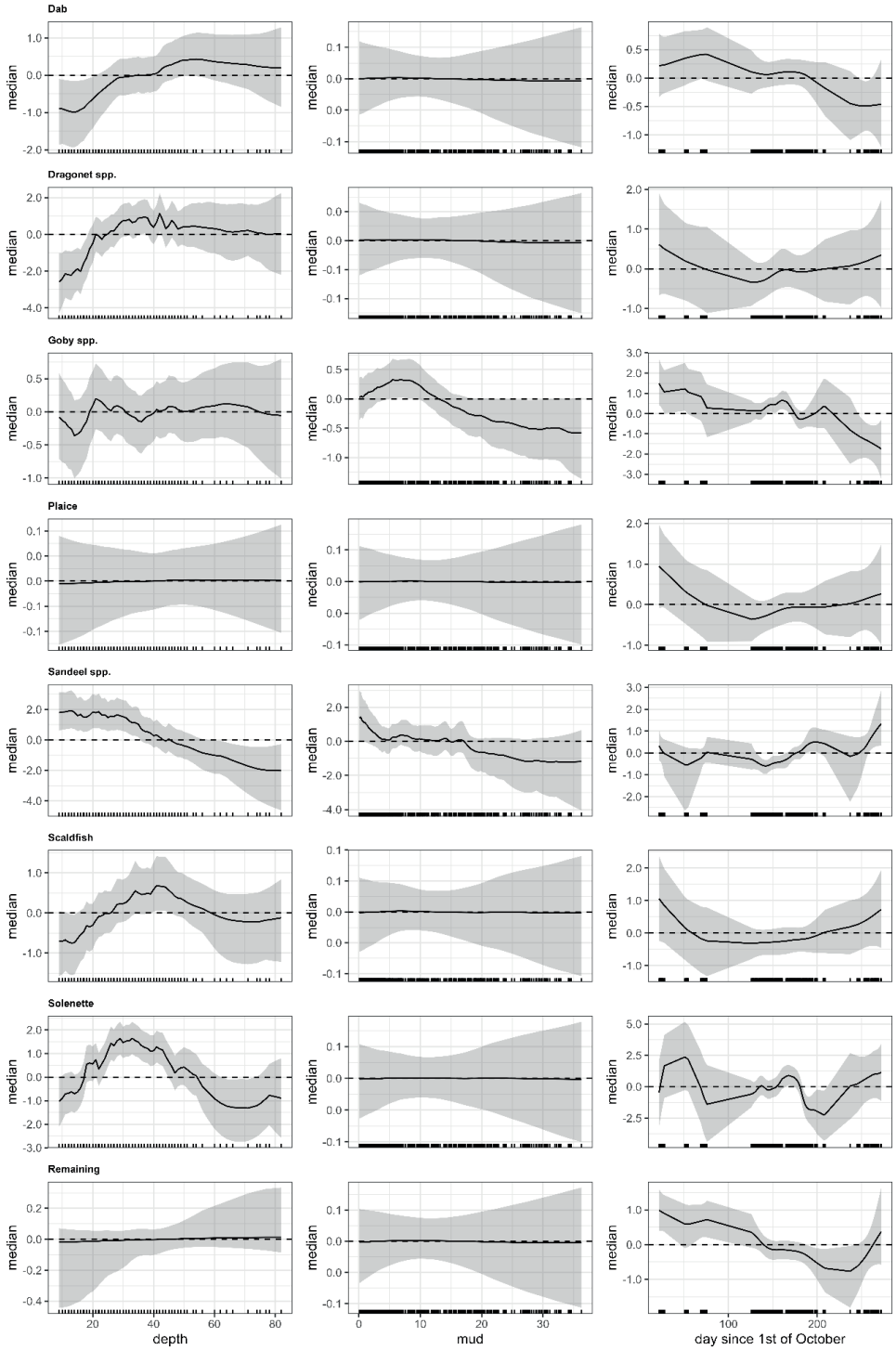


Figure S9: Marginal effects of depth, mud content, and Day of Year (DOY) of biomass per fish species and all remaining species combined, with 95% credible intervals.

Gear comparison based on similar fish communities

Small fish (8-31g) in the southern North Sea

Greenstreet et al. (2007) estimated 'prey' biomass for piscivorous fish in ICES statistical rectangles in the North Sea using IBTS data. Prey was defined as individuals weighing between 8 and 31 g, but sandeel was excluded. For fish meeting this prey criterion, we estimated an average biomass density of 2.7 g m^{-2} (95% CI: 1.5–5.0 g m^{-2}) in the Dutch EEZ and 6.0 g m^{-2} (95% CI: 2.5–14.4 g m^{-2}) in the UK Dogger Bank (Fig. S7). In contrast, Greenstreet et al. (2007) reported biomass estimates ranging from 0.05 to 0.8 g m^{-2}, including a catchability correction factor, for those areas.

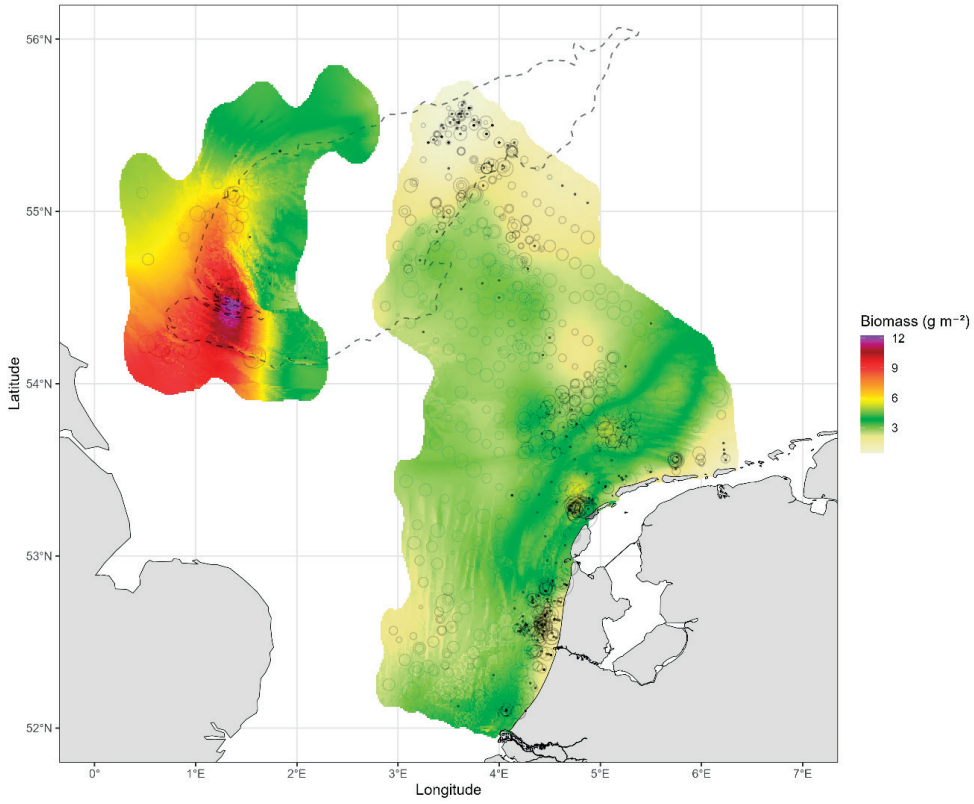


Figure S10: Biomass distribution of fish weighing 8-31 g, sandeel not included, in the southern North Sea. Closed circles represent observations with zero catch, while the size of open black circles corresponds to the observed biomass density per station, corrected for haul distance and sorting fraction.

Seal prey Dutch coastal zone

Aarts et al. (2019) estimated the total fish biomass density of species considered as prey species for harbour seal (bull-rout, cod, common dragonet, dab, fivebeard rockling, flounder, plaice, sandeel, sole and whiting), in the coastal zone north of the Wadden Islands. Nearshore fish densities were determined using data from the DFS survey, while offshore densities were estimated based on BTS data. Their BTS biomass estimation did not include sandeel.

In our study, we estimated biomass densities for the same prey species in both survey areas using the Triple-D dataset. In the DFS survey area, we calculated a biomass density of 7.1 g m² (95% CI: 3.9 - 12.7 g m²; see Fig. S8). Aarts et al. (2019) found an average density of 0.6 g m² for the period 2006-2016 (see supplementary material of Aarts et al. 2019). We also did an estimation without sandeel, since it is known that the DFS is not efficient in capturing sandeel, and estimated a density of 4.0 g m² (95% CI: 2.0 – 8.3 g m^2), which remains considerably higher. When all species caught with the Triple-D dataset are included, notably gobies—which are important prey for seals—we found an average biomass of 11.1 g m² (95% CI: 6.9 – 17.7 g m^2).

Based on the BTS survey, excluding sandeel, an average biomass density of 2.5 g m² was observed for the same period by Aarts et al. (2019). In contrast, our estimate was 6.1 g m² (95% CI: 3.3 - 11.6 g m²). When all Triple-D caught species were included, so with sandeel and gobies, we determined a biomass of 15.1 (95% CI: 9.8 - 23.5) g m².

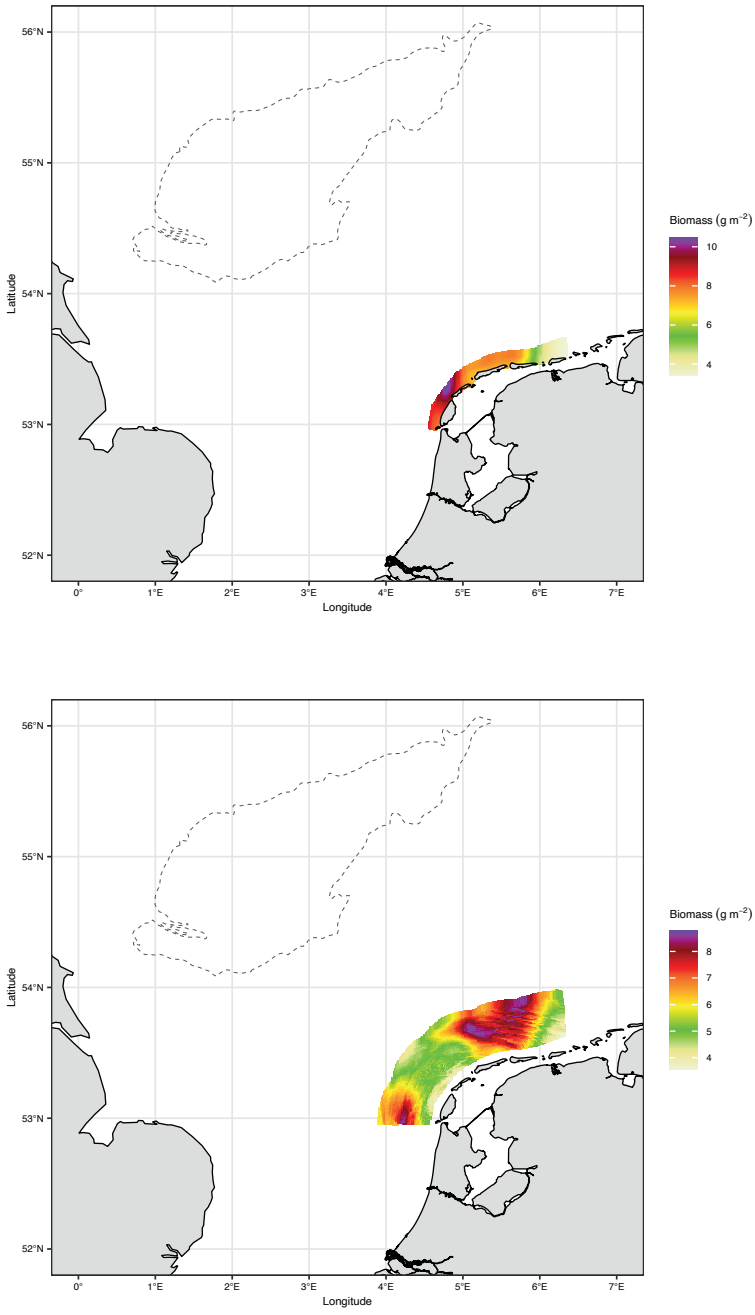


Figure S11: Biomass distribution of summed harbour seal prey in the southern North Sea, with the DFS survey area on the left and the BTS survey area on the right (note that sandeel biomass is not included in the BTS area prediction).

Temporal variation

The Triple-D dataset is not ideal for capturing temporal variation due to limited overlapping sampling points between years across the entire study area. However, in seven regions (see figure below) sampling was conducted multiple times across different years and/or seasons, allowing to examine temporal patterns to some extent.

Figure S13 (bottom panel) shows that, in general, the observed mean biomass for all small (<30 cm) fish species was highest in early autumn, followed by a decline through winter. After winter, biomass increases again. This pattern is particularly evident in the Vlieland area, where the observed biomass in October 2019 was nearly three times higher than in March 2021. Excluding the seasonal effect, no clear annual trend is observed (S13 top panel).

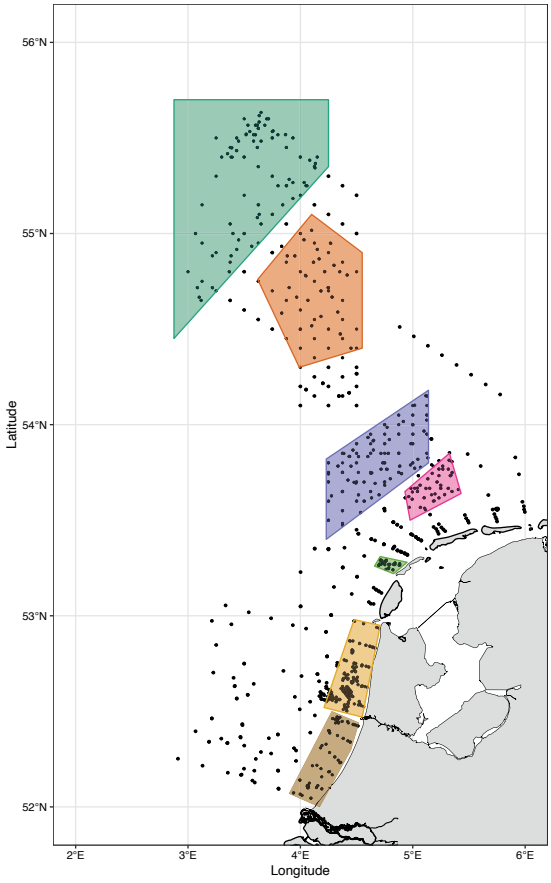


Figure S12: Sampling areas where multiple surveys were conducted. The areas are color-coded as follows: Dogger Bank NL (turquoise), Oyster Grounds (orange), Frisian Front (purple), Frisian Front South (pink), Vlieland (green), Holland Coast North (yellow), and Holland Coast South (brown).

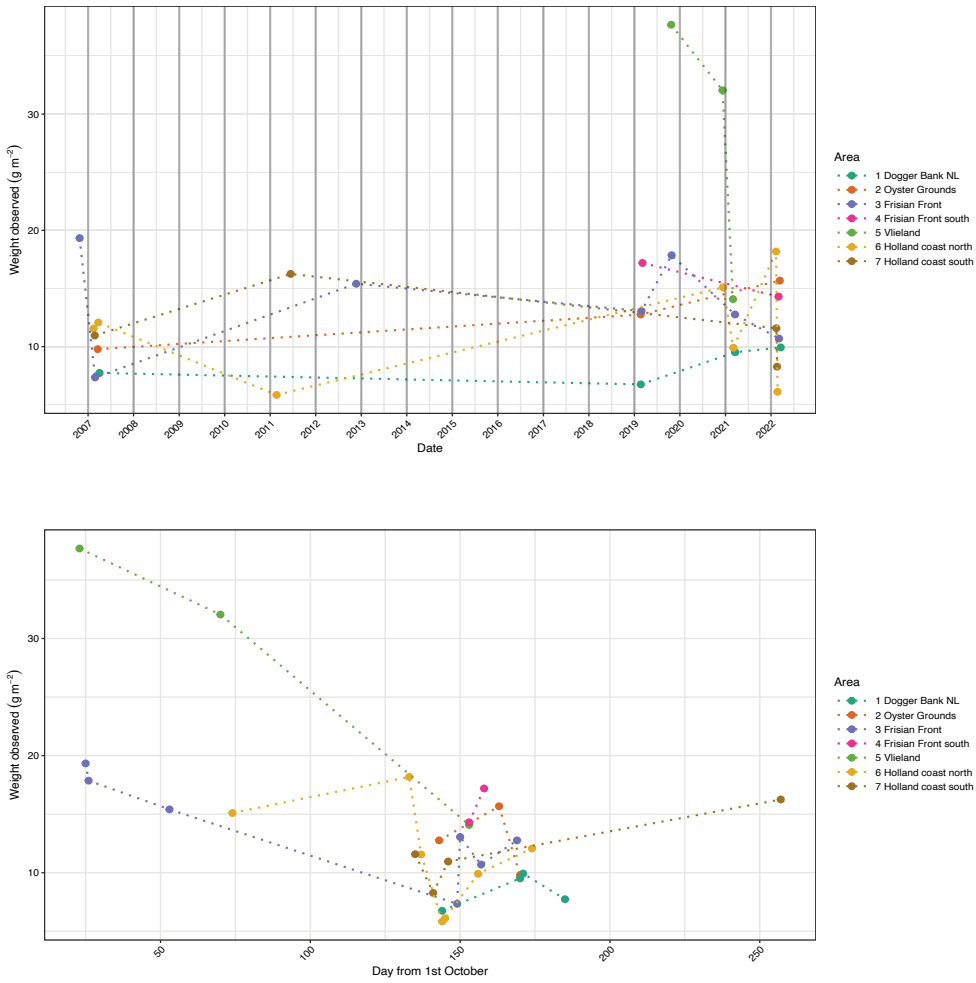


Figure S13: Mean biomass (g m^{-2}) per area for each survey for all small (<30 cm) fish combined. Area colours correspond with figure S12. Top panel: mean biomass per sampling date. Bottom panel: mean biomass per Day Of Year (starting from October 1st).


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Seasonal energy density of sandeel (*Ammodytes* spp.) and other small demersal fish, translated into prey energy landscapes for the Dutch North Sea

Bram Parmentier, Geert Aarts, Sophie Brasseur, Eva Immler, Frank van Langevelde, Ingrid Tulp, Margot Maathuis, Rob Witbaard

ABSTRACT

The availability of prey energy is a key determinant of predator distribution and foraging behaviour. In the North Sea, small demersal fish constitute an important prey base for marine mammals, seabirds, and piscivorous fish, yet species-specific and seasonal energy content data are limited. This constrains the construction of accurate prey energy landscapes that capture variation in prey availability and quality. To address this, we measured seasonal wet-weight energy contents (kJ g^{-1} wet weight) of 10 abundant small demersal fish species from the Dutch North Sea (<30 cm) using bomb calorimetry. The studied species included two sandeel species (*Ammodytes marinus* and *A. tobianus*), dab, dragonet spp., goby spp., plaice, rockling spp., scaldfish, sole, and solenette. Fish were collected in the Dutch North Sea during autumn, early winter, and early spring, with additional sandeel samples from the Wadden Sea in summer. We observed clear seasonal patterns in energy content that differed among species: From autumn (October) to early spring (March) dab, dragonet, plaice, and sandeel declined by ~25%, sole by ~10%, whereas rockling and scaldfish increased by ~10%. Energy contents in gobies increased from early autumn to early winter before declining, whereas solenette and whiting remained relatively stable. Sandeel energy content peaked in summer, rising by ~40% from early spring to mid-summer. No significant differences were found between the two *Ammodytes* species. Species-specific seasonal energy contents were subsequently used to convert biomass maps into prey energy landscapes for individual species and for the total demersal prey community. Our results demonstrate that incorporating species-specific seasonal variation in energy contents improves the ecological relevance of prey energy landscapes for predator–prey studies and ecosystem-based management in the North Sea.

1. INTRODUCTION

Prey availability is a key driver of population dynamics of predators. The presence of sufficient prey determines predator survival and reproduction, and fluctuations in prey abundance are often reflected in predator population sizes (Free et al., 2021; Régnier et al., 2024; Ward et al., 2009). Overlap in predator and prey distribution in space and time is a first prerequisite to enable predators to encounter and catch their prey (Benoit-Bird et al., 2013; Sveegaard et al., 2012). The spatial distribution of prey abundance, referred to as prey landscapes or prey fields, are used to understand the distribution and behaviour of predators (Bedford et al., 2015; Chudzinska et al., 2021; Green et al., 2020; Riaz et al., 2023). Prey landscapes can be best expressed in energy units (see Maathuis et al., 2025a; Ransijn et al., 2019) to account for differences in energy content per unit biomass among prey species (Booth et al., 2023). Considering prey availability in terms of energy, rather than just biomass, provides additional insight into predator foraging decisions and habitat use (Spitz et al., 2012). However, constructing prey energy landscapes for small demersal fish in marine ecosystems is challenging because the energy content values required to convert biomass to energy units are scarce (IJsseldijk et al., 2021; Johnson et al., 2017; Ludwig et al., 2024), and particularly seasonal variation in these values is poorly studied.

In the Dutch North Sea, a variety of small demersal prey species are important for marine mammals, like harbour seals and harbour porpoise (Aarts et al., 2019; Heße et al., 2026; Leopold, 2015). Among the prey species, North Sea sandeel (particularly *Ammodytes marinus*) has been studied relatively extensively in terms of energy content, largely due to their importance for seabirds and their strong link to seabird breeding success (Hislop et al., 1991; Pedersen & Hislop, 2001; Wanless et al., 2018). For many of the remaining small demersal prey species, like gobies (Gobiidae) and dragonets (Callionymidae), energy content data are limited, and have often not been studied in the southern North Sea (Härkönen & Heide-Jorgensen, 1991; Spitz et al., 2010). Furthermore, for solenette and scaldfish, no published energy content estimates are currently available. In addition to these interspecific data gaps, energy content can vary substantially within species depending on area, body size, and season (Albo-Puigserver et al., 2020; Dubreuil & Petitgas, 2009; Pedersen & Hislop, 2001; Wanless et al., 2018; Wuenschel & Bean, 2024). Seasonal variation is linked to reproductive cycles, feeding, and growth (Albo-Puigserver et al., 2020; Pedersen & Hislop, 2001), and because these aspects differ among species, seasonal energy content trends vary across species (Albo-Puigserver et al., 2020).

Ignoring such intraspecific factors may lead to less accurate energy landscape estimates for a given area and season.

To overcome the limited availability of species-specific, regional, and temporal energy content data, we obtained new measurements for 10 small demersal prey species, or taxa, including juvenile dab (*Limanda limanda*), juvenile plaice (*Pleuronectes platessa*), juvenile sole (*Solea solea*), whiting (*Merlangius merlangus*), rocklings (Lotidae), dragonets (Callionymidae), gobies (Gobiidae), sandeels (*Ammodytes* spp.), scaldfish (*Arnoglossus laterna*), and solenette (*Buglossidium luteum*). Additionally, we examined differences between the two *Ammodytes* species (*A. marinus* and *A. tobianus*). These taxa were selected because they form an important part of the demersal diet of predators along the southern North Sea coast (Aarts et al., 2019; Leopold, 2015; Stienen et al., 2000) and were found to be among the most abundant small demersal taxa (Chapter 2)

Prey quality (in terms of energy content) is suggested to be a better determinant of marine mammal foraging strategies than prey quantity alone (Spitz et al., 2012). Therefore, species-specific energy landscapes were created by applying energy content values to the species-specific fish biomass distribution maps produced in Chapter 2. The individual species landscapes were aggregated to construct a total energy landscape of small demersal fish. These landscape energy maps show the spatial distribution of energy density (kJ m^{-2}). Energy density is also commonly used in the literature to refer to energy per unit biomass (see e.g. Dubreuil & Petitgas, 2009; Wuenschel & Bean, 2024). To avoid confusion, in this study we use "energy content" to refer specifically to energy per unit body mass, and "energy density" to refer to energy per unit surface area.

Prey energy landscapes in combination with predator distribution and movement data can reveal whether predator distributions and foraging patterns are primarily driven by (species-specific) prey availability or whether other factors, such as human infrastructure and activities, also play a role. This information can be used to guide management actions, for instance by minimizing anthropogenic pressures in key prey areas. For example, sandeel fisheries have been closed along parts of the Scottish coast since the early 2000s, and at the Dogger Bank since 2024, due to concerns about negative impacts on seabirds and the wider ecosystem (Daunt et al., 2008; ICES, 2025b; Searle et al., 2023).

2. METHODS

2.1. Fish collection

During four cruises in 2019-2022 with RV Pelagia and Arca 229 stations were sampled for benthos and small demersal fish on the Dutch Continental Shelf. The NIOZ Deep Digging Dredge (Triple-D) was used (Bergman & van Santbrink, 1994), which has a 7 x 7 mm mesh size and captures small demersal fish (<30 cm) within and up to 20 cm above the seafloor. Sampling took place in October 2019, December 2020, March 2021 and February/March 2022.

In addition, the inlets between the North Sea and the Wadden Sea were monthly sampled from March 2021 to March 2022 by a stow-net survey targeting clupeids and pelagic sandeel (Maathuis et al., 2025b). The stow-net is a passive fishing gear that samples the entire water column (average depth 5.3 m) during periods of strong tidal currents, both during incoming and outgoing tides. The net is held open by two 8 m beams and has a stretched mesh size of 20 mm in the codend (see Maathuis et al., 2025b for further details).

For both sampling methods, fish were sorted from each catch, identified to species level, measured, weighed, and frozen at −20 °C. A total of 369 small demersal fish were selected for energy content analysis (see Section 2.3). Species were chosen either because they are important in the diet of harbour seals along the Dutch coast (Aarts et al., 2019; cod and bullrout were excluded due to low catch numbers in the Triple-D survey) or because they are among the most abundant small demersal species in the Dutch EEZ, such as solenette (see Chapter 2). The selected fish included 13 dab, 23 dragonets, 34 gobies, 12 plaice, 12 rocklings, 231 sandeels (100 from the tidal inlets), 12 scaldfish, 11 sole, 11 solenette, and 10 whiting. Efforts were made to cover the full length range (up to 30 cm) of each species. Samples were also distributed evenly across three sampling periods (early autumn, early winter, and late winter/early spring), without targeting specific geographic locations (see Figure S1). From the late winter/early spring 2021 Triple-D survey, only sandeel were selected for energy content measurements, whereas in late winter/early spring 2022 campaign only non-sandeel species were selected. Monthly sample sizes of sandeel from the Wadden Sea stow-net survey varied considerably due to fluctuations in catch numbers, so some months were better represented than others.

2.2. Sandeel species identification

Two *Ammodytes* species occur in the Dutch coastal North Sea: the lesser sandeel *Ammodytes marinus* and the small sandeel *Ammodytes tobianus* (Tien et al., 2017). They can be distinguished by morphological traits (Macer, 1966;

Reay, 1970) but accurate identification is challenging (Heessen et al., 2015; Nævdal & Thorkildsen, 2002). Therefore, DNA-based techniques (sequence or qPCR) are used to reliably identify them (see Chapter 4). Only those confirmed by DNA (n = 187) were included to test for species-specific differences in energy content.

2.3. Energy content

Selected fish were thawed, measured for length and wet weight, after which they were freeze-dried for a minimum of 72 hours at −50 °C and 0.02 mbar. The freeze-dried fish were then ground into a fine powder, and 0.5 g samples were compressed into pellets. If an individual fish contained less than 0.5 g of fish powder, benzoic acid was added to reach the required 0.5 g. Gross energy content (J g^{-1} dry weight) was determined using an IKA C2000 bomb calorimeter, which quantifies the heat released during combustion of the pellets. Individual wet-to-dry weight ratios were used to convert the measurements from dry weight to energy content per gram wet weight.

2.4. Statistical analysis

The relation between season and energy content (kJ g^{-1} wet weight) was analysed using generalized additive models (GAMs) assuming a Gaussian distribution for the response variable (see figure S2). Energy content was modelled as a smooth function of week, where week 0 was set to 1 October to align the temporal trend with the onset of winter. To allow species-specific seasonal patterns, a factor-smooth interaction was included (bs = "fs"), which fits a separate smooth of week for each species. Predicted values and standard errors were then obtained from the fitted GAM.

Albo-Puigserver et al. (2020) found that a condition factor (weight/length^3) can capture seasonal variability in energy content for anchovy and sardine. To test whether this also applies to the small demersal species, we fitted a similar GAM to the energy content model but with condition factor as the response variable. Condition factor as a proxy for energy content could provide a more labour- and cost-efficient alternative to direct measurements of energy content.

For sandeel (*Ammodytes* spp.), we extended the model by including either absolute length or relative length (i.e., relative to the mean length of all sandeel caught within the same period of the year) as an additional explanatory variable, as previous studies have shown that energy content increases with (relative) length sandeel and other species (Dubreuil & Petitgas, 2009; Hislop et al., 1991; Tirelli et al., 2006). The smooth of 'Length' or 'Relative length' was included as a thin plate regression spline with penalized null-space (bs = "ts").

For sandeel, species-specific differences in energy content between the two *Ammodytes* species (*A. marinus* and *A. tobianus*) were investigated. Because only a few *A. marinus* individuals were collected in the Wadden Sea, this analysis was restricted to North Sea samples where both species occurred in roughly equal numbers. Energy content was modelled using a GAM and included species, month (treated as a categorical factor), and their interaction as parametric explanatory variables; no smooth terms were included. Finally, for *A. tobianus* we tested whether energy content differed between the North Sea and the Wadden Sea with the two regions as a categorical factor variable. This was done to determine whether sandeel from both regions could be combined to construct a year-round trend. This analysis was limited to data from March 2021, when sandeel were collected in both the North Sea and the tidal inlets.

2.5. Energy landscapes

To construct an energy landscape, spatially explicit information on biomass distribution is required, which can be converted into energy density per unit area using species-specific and seasonal-specific energy contents. For small demersal fish biomass, we used estimates from Chapter 2 where predicted wet-weight biomass distribution for the seven most abundant (based on biomass) small demersal fish taxa—sandeels, gobies, dragonets, dabs, plaice, scaldfish, and solenette—and all remaining species aggregated in a separate group. Because in Chapter 2 we provided biomass estimates for late February, we used therefore the corresponding species-specific energy content values for this time period to convert biomass maps into energy maps. For the remaining fish in the aggregated fish group, we assumed an average energy content based on rockling, sole, and whiting, which were the most abundant species within this remaining species group (see Supplement Chapter 2). In contrast to Parmentier et al. (2025), who produced a total small demersal biomass map by spatially modelling summed biomass observations across all species at each station, we aggregated the individual species-specific energy landscapes to create a total prey energy landscape. This approach accounts for interspecific variation in energy content and thus provides an energy-weighted representation of prey availability.

3. RESULTS

3.1. Energy content

Mean energy content per species (ordered from low to high) was: whiting 3.8 ± 0.9, plaice 4.2 ± 0.8, rockling spp. 4.3 ± 0.6, goby spp. 4.7 ± 0.8, dab 4.8 ± 0.9, sandeel spp. 5.0 ± 0.7, dragonet spp. 5.1 ± 0.7, scaldfish 5.2 ± 0.5, sole 5.4 ± 0.6, and solenette 5.4 ± 0.5 kJ g^{-1} wet weight (see Table S1). The large standard deviations indicate substantial variability around the mean, which was largely driven by species-specific seasonal variation captured by the smooth function of week (GAM; $p < 0.001$, $F = 6.115$). From autumn (October) to early spring (March), energy content trends differed among species (Figure 1). Dab, dragonet, plaice, sandeel, and sole exhibited declines in energy content over this period. Mean values dropped by approximately 25% for all species except sole, whose energy content decreased by about 10%. In contrast, rockling and scaldfish showed a 10% increase over the same period. The energy content of gobies increased from early autumn to early winter followed by a decline. The energy content of solenette and whiting remained relatively stable throughout the overwintering period.

For sandeel (*Ammodytes* spp.), a summer trend could also be constructed, although the number of individuals measured in midsummer was low. Energy content increased by 40%, from an estimated mean of 4.25 (4.07-4.43) kJ g^{-1} wet weight in week 25 (counting from October; March) to 6.03 (5.72-6.33) kJ g^{-1} wet weight in week 43 (counting from October; July). This increase was followed by a decline throughout autumn and winter. Next to the seasonal effect, absolute length also explained the observed variation in energy content (GAM; $p = 0.0195$, $F = 1.356$), with individuals of approximately 13 cm showing the highest energy content (Figure S3). However, the effect of length was much smaller than that of season. Relative length, represented by length relative to all other measured sandeel individuals within a sampling week, did not contribute to explaining energy content after accounting for seasonal variation (GAM; $p = 0.94$, $F = 0.0$).

No significant differences in energy content were observed between the two *Ammodytes* species (*A. marinus* and *A. tobianus*) across sampling months in the North Sea (Figure 2). The sandeel model indicated that neither the main effect of species (GAM; $p = 0.635$) or the species × month interactions were significant (GAM; all $p > 0.395$). However, a comparison of *A. tobianus* individuals caught in March 2021 in the North Sea versus the Wadden Sea inlets indicated slightly lower energy content in the Wadden Sea (−0.23 kJ g^{-1}), but this difference was not statistically significant (GAM; $p = 0.103$) (Figure 2).

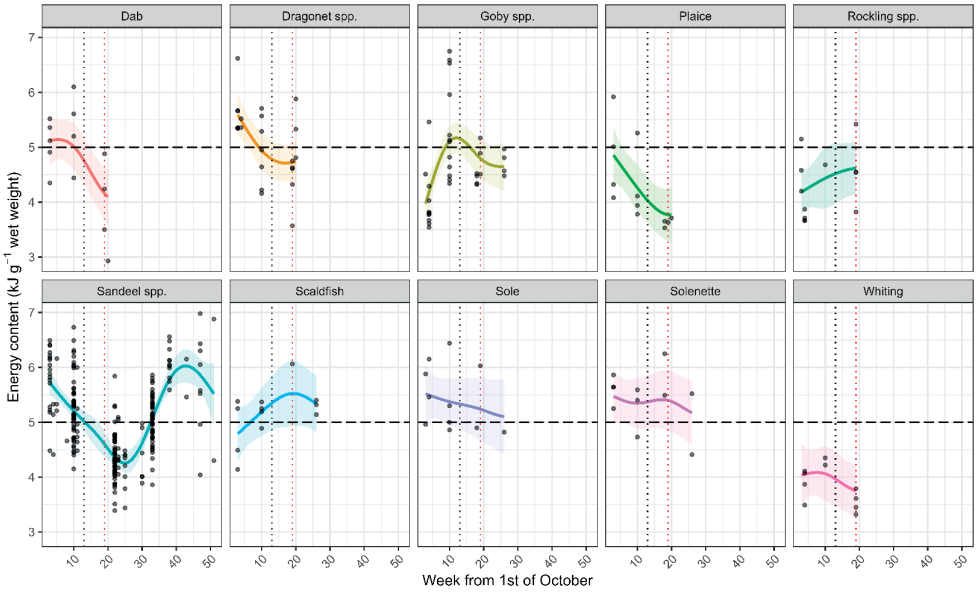


Figure 1: Estimated energy content (kJ g^{-1} wet weight) of small demersal fish from 1 October onward (coloured line) with 95% confidence intervals (shaded area). Individual measurements are shown as black dots. The black dashed line indicates 1 January, and the red dashed line indicates week 19 (early February).

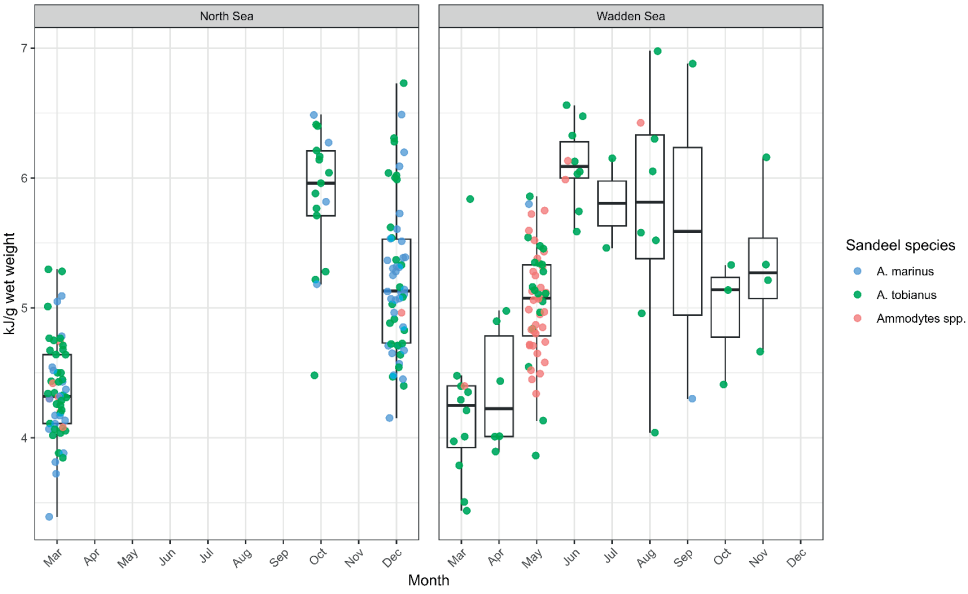


Figure 2: Boxplots with individual data points showing sandeel energy content (kJ/g wet weight) of the two *Ammodytes* species (*A. marinus* and *A. tobianus*) collected in different months (and years) from the North Sea and the Wadden Sea inlets.

3.2. Energy landscapes

Using the estimated species-specific and seasonal energy contents, species-specific energy landscapes were constructed. Predicted mean energy content values for winter (February, week 19: Figure 1; Table S1) were used to convert the biomass maps of Chapter 2 into energy landscapes (Figure 3). Since we did not observe clear spatial heterogeneity in energy content (see Figure S4 for sandeel spp.), we assumed no spatial heterogeneity in energy content. The limited data available for other species also did not reveal clear spatial patterns (figures not shown). Consequently, the spatial structure of the energy landscapes for each species was identical to that of the species-specific biomass maps. However, differences in energy contents among species (ranging from 3.75 kJ g^{-1} for whiting to 5.52 kJ g^{-1} for scaldfish) changed the relative contribution of each species to the overall energy landscape map compared with the original overall biomass maps.

Figure 3 shows the modelled winter (February) energy density per unit area distribution for the seven most abundant small demersal fish species, together with the aggregated group of remaining species. Dab, plaice, and the remaining species exhibited a relative uniform distribution of energy density. In contrast, energy densities of dragonets and gobies were highest in the southern North Sea (south of 54°N), with estimates reaching up to 20 and 25 kJ m^{-2}, respectively. However, dragonets exhibited low energy densities (<4 kJ m^{-2}) in nearshore areas. Solenette showed similarly low nearshore energy densities but, unlike dragonets and gobies, reached high energy densities (up to 20 kJ m^{-2}) at the Dogger Bank. Scaldfish exhibited the highest energy densities in the central parts of the Dutch EEZ, where sandeel was almost absent. In contrast, sandeel energy densities were concentrated in coastal areas and at the Dogger Bank, with a hotspot along the western Wadden Islands reaching up to 49 kJ m^{-2}.

Figure 4 shows the resulting fish energy landscape of all small demersal species aggregated across the Dutch EEZ. In this area, the mean energy value is 67.5 kJ m^{-2}, but ranges from approximately 25 kJ m^{-2} on the northern Dogger Bank to a maximum of 150 kJ m^{-2} northwest of the Wadden Islands. The map shows that low-energy areas are found along the western coastal mainland and in the deepest part of the central Oyster Ground, centred at 54.2°N.

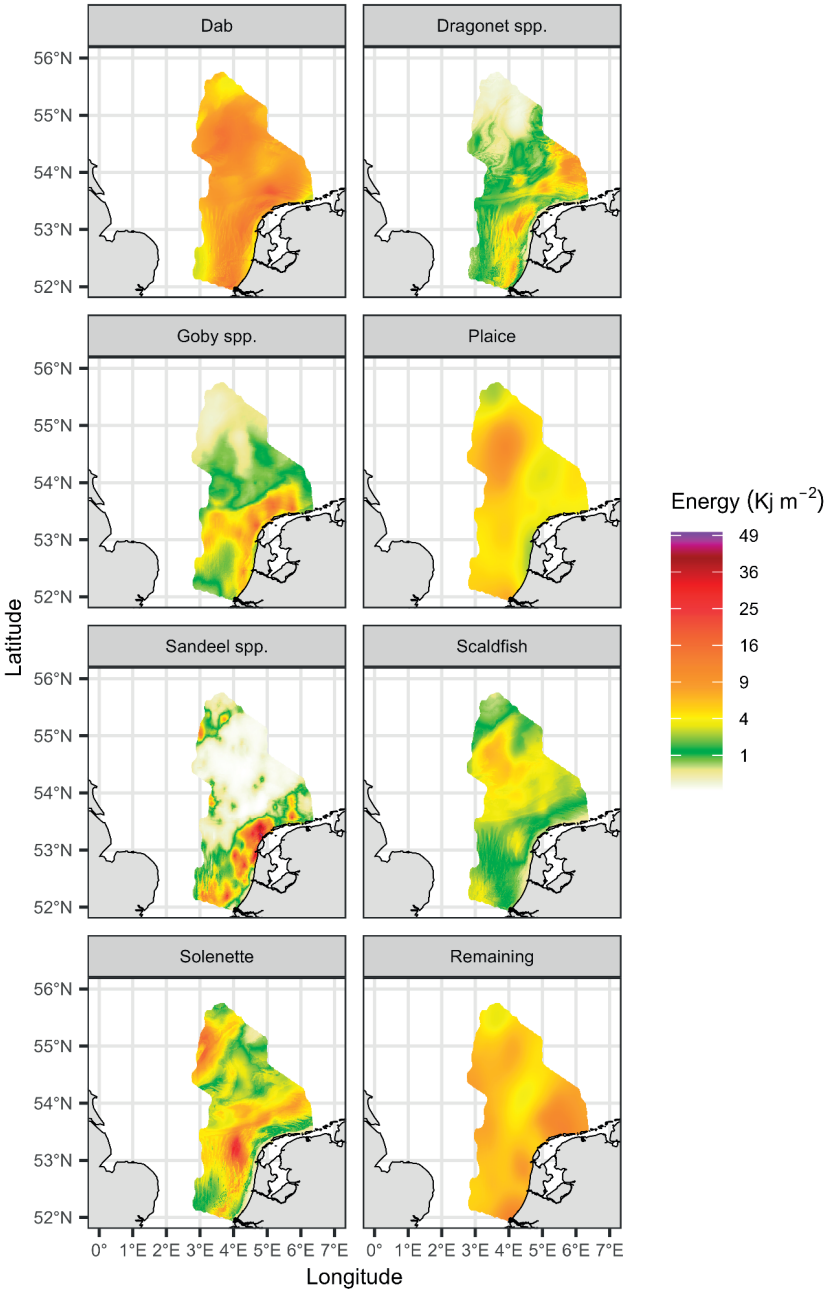


Figure 3: Energy densities (kJ m^{-2}) per species in February. Note the quadratic scale.

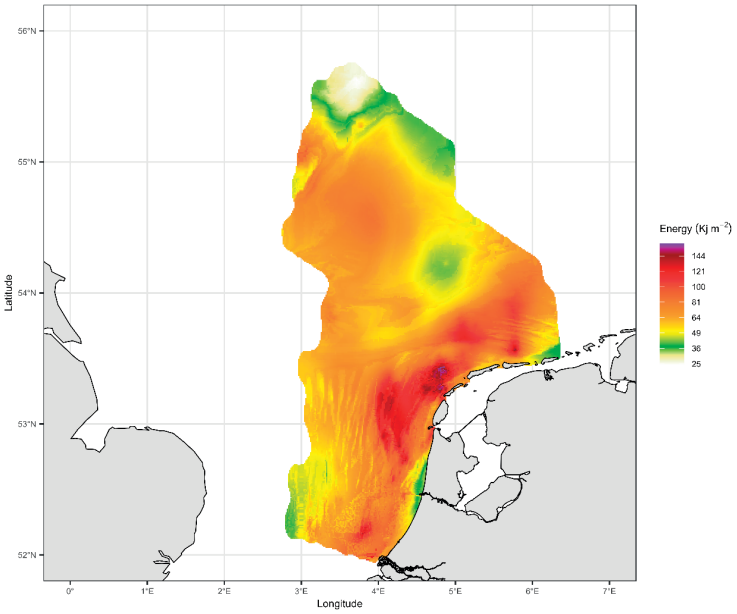


Figure 4: Total energy density (kJ m^{-2}) for small demersal fish in February. Note the quadratic scale.

4. DISCUSSION

In this study, we quantified species-specific and seasonal wet weight energy contents of small demersal fish, with a particular focus on sandeel. Winter values were then used to construct both species-specific and aggregated energy landscapes representing the total energy available from small demersal fish in the Dutch North Sea.

4.1. Seasonal trends

The species-specific energy contents determined for this study were generally consistent with previously reported values (Figure S5). This study as well as earlier studies showed considerable variability. However, this study revealed substantial seasonal variation in energy content year, with overwinter trends differing among species. For instance, plaice and scaldfish had similar estimated mean energy contents in autumn, namely 4.85 (4.36–5.36) and 4.78 (4.29–5.29) kJ g^{-1} wet weight, respectively. While in spring the differences were substantial, with plaice containing 3.77 (3.24–4.28) and scaldfish 5.33 (4.82–5.85) kJ g^{-1}. These results demonstrate that seasonal timing of sampling is a crucial factor in determining whether the observed energy contents differ among species. Furthermore, the observed seasonal patterns in wet-weight energy content resulted from seasonal variation in both energy content per gram of dry weight and the dry-to-wet weight ratio (see Figures S6 and S7). It should be noted that

sample sizes were limited (except for sandeel), and sampling did not occur in consecutive months within the same year, therefore, interannual effects cannot be excluded as a factor contributing to the observed seasonal variation.

For sandeel, a year-round trend could be constructed, due to additional monthly samples from the Wadden Sea inlets. The data showed that energy content was lowest in March–April, thereafter the energy content increased to a peak in mid-summer, followed by a decline throughout autumn and winter. This pattern is consistent with the March–June energy content values presented in Appendix 1 in Hislop et al. (1991) or with the annual pattern found in lipid percentage of northern sandeel (*Ammodytes dubius*) in the Northeast US shelf (Suca et al., 2021). The observed seasonal pattern reflects the sandeels' spring and summer foraging season and subsequent winter hibernation. During hibernation sandeel do not forage in the water column and rely entirely on body energy reserves (Henriksen et al., 2021; van Deurs et al., 2010; Winslade, 1974b). They also invest in reproduction while buried, and are therefore considered as extreme capital breeders (Wright et al., 2017). Hence, their energy content gradually decreases over winter, likely more strongly than in the other species due to their capital-breeding strategy.

Seasonal patterns in energy content of the small demersal species other than sandeels have not been studied previously, as most studies cover only a single sampling period (e.g., autumn in Spitz et al., 2010). In contrast, seasonal variation has been documented for other fish species, such as Norway pout, saithe, herring, anchovy and sardine (Albo-Puigserver et al., 2020; Dubreuil & Petitgas, 2009; Pedersen & Hislop, 2001). Albo-Puigserver et al. (2020) similarly showed that seasonal trends in energy content are species-specific: energy content was lowest in autumn for anchovy, whereas for sardine it was lowest in winter. They attributed these differences to contrasting strategies of energy acquisition and allocation for reproduction, with anchovy exhibiting an income-breeder strategy (i.e. gonad development during the foraging season) and sardine a capital-breeder strategy (i.e. gonad development after the foraging season). We did not examine the influence of gonad investment or reproductive strategy on energy content in this study.

Albo-Puigserver et al. (2020) also showed that body condition can serve as an alternative proxy to capture seasonal variability in energy content. In our study, the condition factor (weight/length^3) displayed seasonal patterns comparable to those of energy content for dab, plaice, rockling spp., sandeel spp., and whiting (Figure S8). In contrast, such patterns were less evident for dragonet spp., goby spp., scaldfish, sole, and solenette. Nevertheless, the comparable

seasonal trends in energy content and condition factor for at least some species suggest that body condition can serve as a less labour-intensive proxy for energy content.

4.2. Remaining variation

The seasonal patterns were characterised by a strong variability around the trend in all species (Figure 1). This variation may arise from factors such as fish length, sampling year and spatial heterogeneity (Dubreuil & Petitgas, 2009; Hislop et al., 1991; Wuenschel & Bean, 2024). Mapping energy contents of sandeel per season did not reveal a spatial signal in the North Sea (Figure S4). Furthermore, no significant differences were found between sandeel energy content values of the North Sea and the Wadden Sea inlets. These findings suggests that spatial variation at the scale of this study had little influence on the measured energy contents. For the other studied species, no consistent spatial patterns were observed either (figures not shown), although sample sizes were limited.

Energy content has been shown to increase with relative length (i.e. length within the same period of the year) for anchovy and sandeel (Dubreuil & Petitgas, 2009; Hislop et al., 1991; Tirelli et al., 2006). With the exception of sandeel, our data did not indicate a similar size-related increase in energy content for the species and size range analysed in this study (Figure S9). For sandeel, the effect of relative length within a sampling week was tested explicitly, but we did not find a significant effect. A possible explanation for this discrepancy with Hislop et al. (1991) is that our study covered not only spring and summer months but also autumn and winter. This broader seasonal coverage is important, as sandeel spawn during winter (*A. marinus*) or autumn/spring (*A. tobianus*) (Reay, 1970), which may obscure length-related effects on energy content: some large individuals may have already spawned while others have not. During spawning, a substantial amount of energy is released from the body, which will lower the average energy content of the fish. Consequently, the effect of relative length can disappear when gonad stage is not taken into account.

Sandeel sampled in the summer months were generally larger (Figure S9), likely due to the larger mesh size used during those surveys (20 mm versus 7 mm). To assess whether the observed seasonal pattern in energy content could be attributed to body size, we extend the model by including the effect of absolute length. Although length had a small effect on energy content, the seasonal effect remained strong, indicating that the observed seasonal patterns exist independently of body size.

In this study, we found species-specific differences in both absolute energy contents and seasonal trends in the energy contents. However, within the *Ammodytes* genus, no significant differences were detected between *A. marinus* and *A. tobianus* sampled in the North Sea within the same year and month. For other grouped taxa, such as dragonets and gobies, species-specific differences may exist, but we did not investigate this due to relatively low sample sizes.

4.3. Energy landscapes

Energy content per unit biomass differed among species, for example, whiting had a general low energy content, whereas sandeel and gobies energy content was nearly twice as high at some moments in the year. Consequently, energy landscapes based on species-specific energy contents provide a more accurate representation of prey availability than biomass distributions. Prey energy landscapes can be used to better understand predator distributions and foraging trips (e.g. Chudzinska et al., 2021). By linking predator distribution and foraging behaviour to species-specific and aggregated energy maps, it might be possible to assess whether predators preferentially select particular prey species, whether observed patterns are driven by total small demersal fish energy availability, or whether other prey-related factors play a role.

Besides energy content, other prey traits, such as the fatty acid content and composition, may also influence prey choice. Specific fatty acids have been shown to enhance health, growth, and reproductive output in marine predators (Lin et al., 2023; Scharnweber & Gardmark, 2020). Fatty acid composition differs among prey species (Gladyshev et al., 2018), therefore it would be beneficial for predators to selectively target species with high fatty acid levels. Hence, linking spatial maps of fatty acid content with predator foraging behaviour could provide further insight into whether this is an important prey attribute and how it influences foraging behaviour.

A limitation of the presented energy landscapes is that they represent prey energy availability at a single point in time (winter), as biomass estimates were predicted for February. Preferably, energy production maps would be constructed, showing the spatial patterns of energy productivity throughout the year rather than as a single snapshot. Such maps would need to incorporate species-specific growth rates, the net effects of migration, and the spatial input of new cohorts (e.g., from nursery areas). However, mapping all of these processes at a small spatial scale is challenging, as much of this information is unknown, particularly for small non-commercial species. Nevertheless, total productivity and standing biomass are generally correlated (Randall & Minns, 2000), so

using standing biomass, and thus standing energy, as a proxy for productivity provides a practical and simplified representation of prey energy availability.

Comparing our energy landscapes and densities with those from other studies in the North Sea region (e.g. Maathuis et al., 2025a; Ransijn et al., 2019) seems challenging, as these other studies considered different prey assemblages, applied different species-specific energy values, or relied on alternative biomass estimates. For example, both Ransijn et al. (2019) and Maathuis et al. (2025a) included pelagic species such as herring and sprat, which were not considered in our study. Consequently, both absolute values and spatial patterns are expected to differ between their results and ours. However, future work could integrate the complementary (demersal + pelagic; small and large fish) components of the different studies to provide a more complete picture of prey energy availability in the southern North Sea.

4.4. Implications

In this study, we showed that small demersal fish exhibit species-specific seasonality in energy content per gram wet weight. For some species, energy content increased by up to 40% between the periods with lowest and highest energy content, whereas for other species it remained relatively stable. Therefore, seasonal and species-specific variation in energy content should be considered when estimating available prey energy.

Prey of low nutritional quality but high abundance are sometimes referred to as 'junk food', and high consumption of such prey by predator species has been suggested to negatively affect population health (Osterblom et al., 2008). Gobies and small gadoids (e.g. whiting) have been suggested to act as 'junk food' for harbour porpoises in the southern North Sea by filling the stomach without providing sufficient energy (IJsseldijk et al., 2021). However, our data show that this classification is not consistent across all seasons for gobies. While they exhibit low energy contents in autumn, their energy content is higher in other periods and can even exceed that of sandeel in early spring. In contrast, whiting reveal low energy contents year-round and may therefore function as 'junk food', which may quickly fill the stomach without meeting energetic requirements (IJsseldijk et al., 2021). Thus, these findings highlight that seasonality plays a key role in determining whether a prey species acts as 'junk food'. Additionally, seasonal and species-specific variation in energy content is also important when assessing predation pressure (Aarts et al., 2019), feeding preferences (Ludwig et al., 2024) or parameterising bioenergetic models (Booth et al., 2023).

Accurate energy landscapes can help to understand how predators use the area for foraging. For instance, when predator foraging patterns differ from those expected based on prey energy availability, this could indicate that other factors (e.g. catch effort, prey processing time, or fatty acid content) may influence prey selection. Alternatively, mismatches between prey availability and predator foraging may point to the importance of other, non-food-related drivers, including anthropogenic pressures such as offshore wind farms or areas with high underwater noise influencing foraging efficiency. These insights are valuable for ecosystem-based management and spatial planning, as they can guide measures to reduce anthropogenic impacts, for example by (seasonally) avoiding key foraging areas when planning locations for wind farms or shipping routes.

Acknowledgements

This work was funded by the Netherlands Organisation for Scientific Research (NWO) through Top Sector Water & Maritime under the project "Forage Fish" (NWOTWM.81.019.008). The UK Dogger Bank sampling, as well as the contribution of G. Aarts and S. Brasseur to this manuscript, were funded through HORIZON EUROPE program ACTNOW: Advancing understanding of Cumulative Impacts on European marine biodiversity, ecosystem functions and services for human wellbeing (Grant no. 101060072). We thank all assistants and colleagues from NIOZ for their help during the North Sea data collection surveys. We are grateful to the crews of *De Arca* from Rijkswaterstaat and RV *Pelagia*. We also acknowledge the support of Jurre Kerkhof and WMR colleagues on board the ZK1 during sandeel sampling in the Wadden Sea. Finally, we thank Dominique Boer and Simon Boon for their extensive laboratory work.

SUPPLEMENT MATERIAL

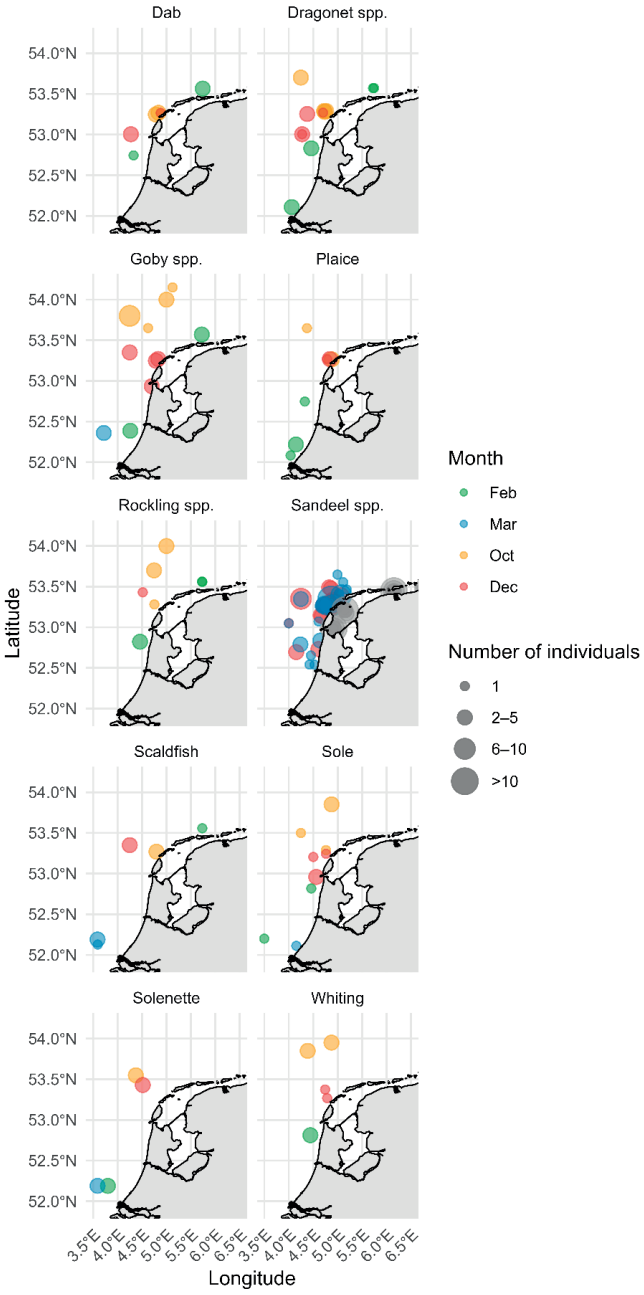


Figure S1: Sampling locations of fish for which energy content was determined. Colours indicate the sampling month, grey dots represent year-round sandeel sampling locations in the Wadden Sea, and dot size corresponds to the number of individuals of a given species collected at each location.

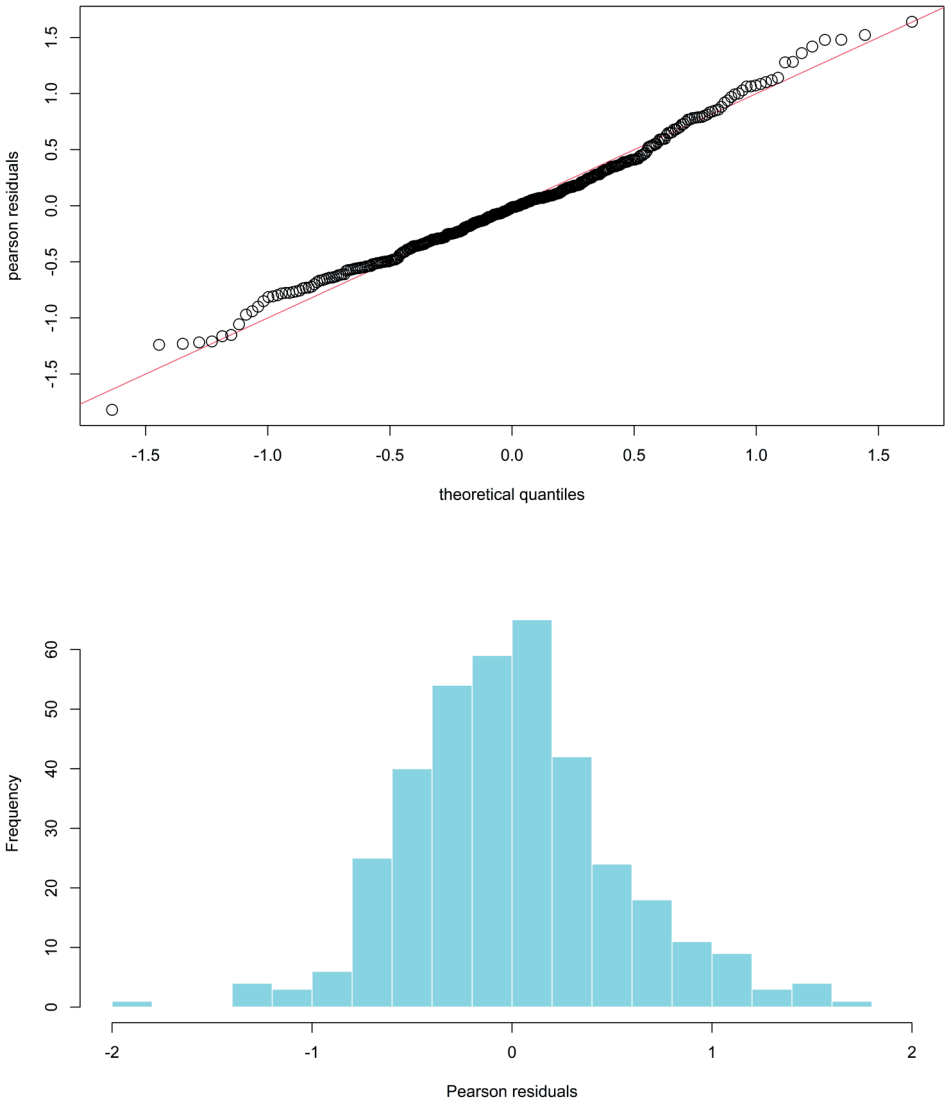


Figure S2: Top: Q–Q plot of the GAM model with a species-specific week smoother. Bottom: Histogram of the Pearson residuals of the same model.

Table S1: Estimated energy content (kJ g^{-1} wet weight) for the ten small demersal fish species in February (week 19). Given are the predicted mean values and their 95% confidence limits.

	Energy content kJ g^{-1} wet weight		
Taxa	**Mean**	**CI lower limit**	**CI upper limit**
Whiting	3.75	3.26	4.24
Plaice	3.77	3.28	4.25
Dab	4.16	3.68	4.63
Sandeel spp.	4.60	4.37	4.83
Rockling spp.	4.62	4.13	5.11
Dragonet spp.	4.72	4.37	5.07
Goby spp.	4.80	4.45	5.15
Sole	5.24	4.67	5.81
Solenette	5.40	4.85	5.95
Scaldfish	5.52	4.92	6.13

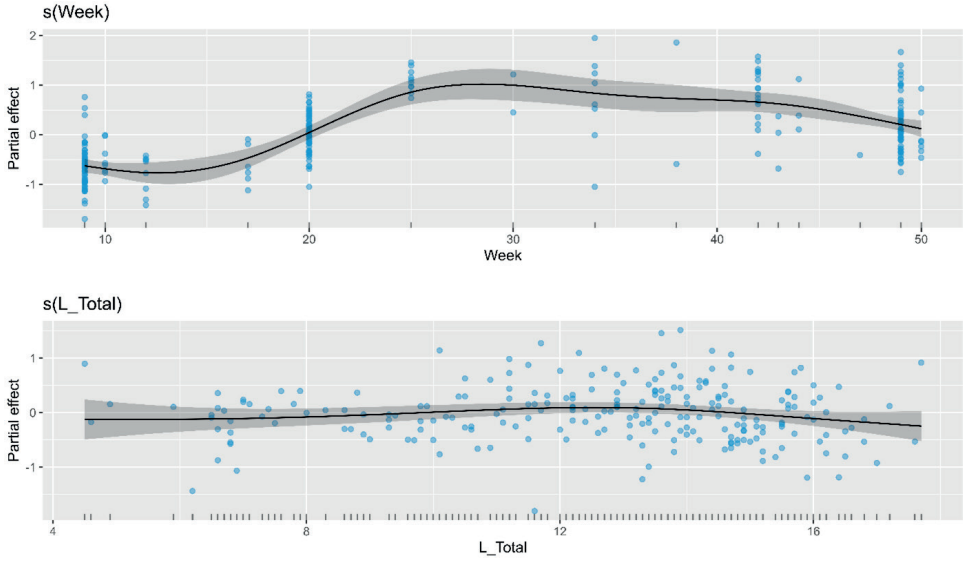


Figure S3: Partial effects of week and total length on sandeel energy content (kJ g^{-1} wet weight).

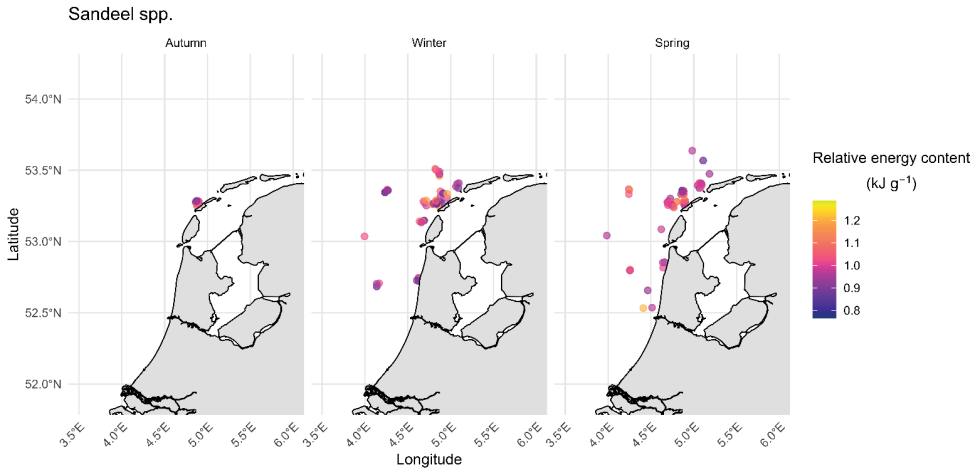


Figure S4: Relative energy content per season (kJ g^{-1}) of sandeel spp. collected in the North Sea.

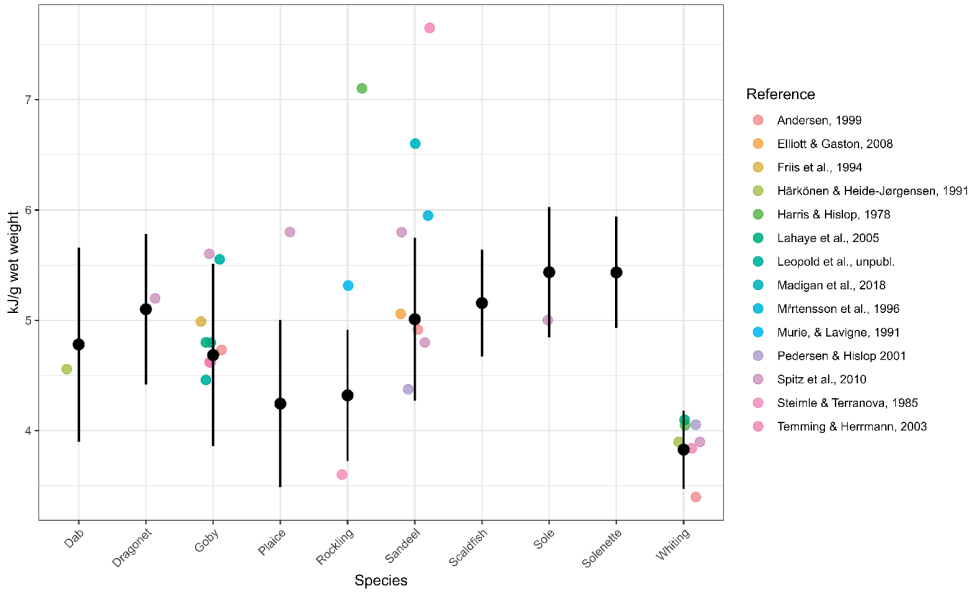


Figure S5: Species-specific energy contents. Values from this study are shown in black (mean ± SD). Additional energetic values are derived from the literature, based on the overview compiled by IJsseldijk et al. (2021).

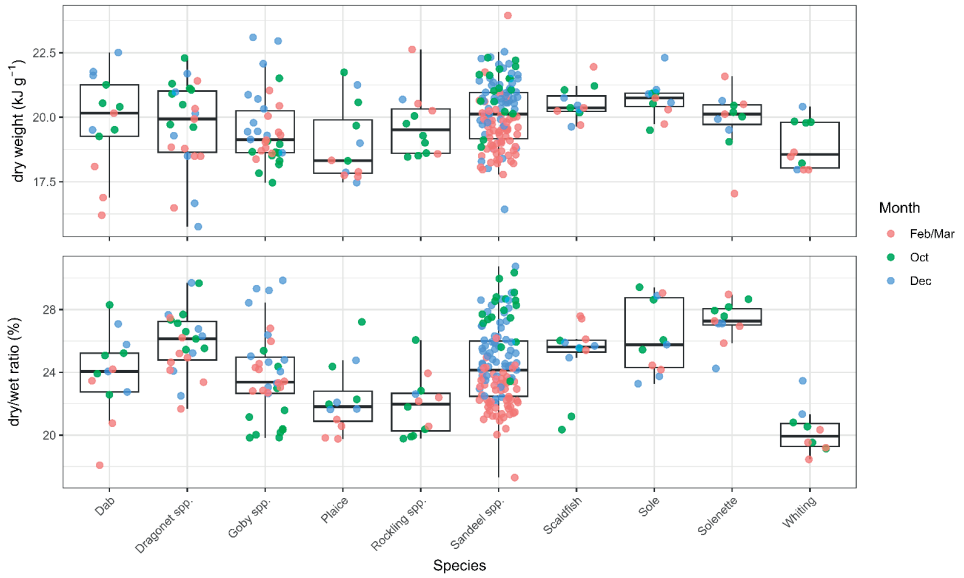


Figure S6: kJ g^{-1} dry weight (top) and dry/wet weight ratio (bottom) per species coloured by month.

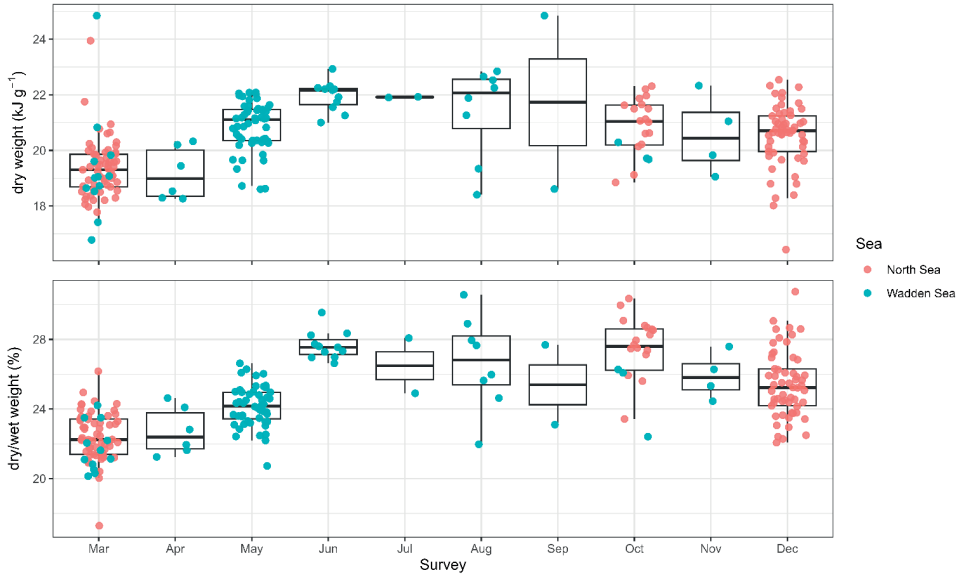


Figure S7: kJ g^{-1} dry weight (top) and dry/wet weight ratio (bottom) of sandeel spp. coloured by sampling location.

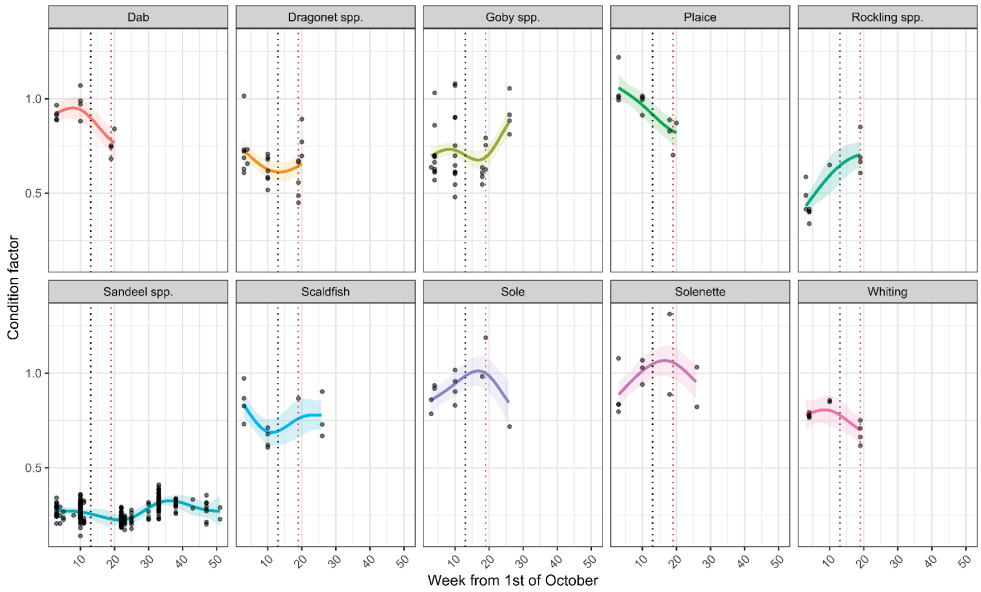


Figure S8: Estimated condition factor (weight/length³) per species. Individual measurements are shown as black dots.

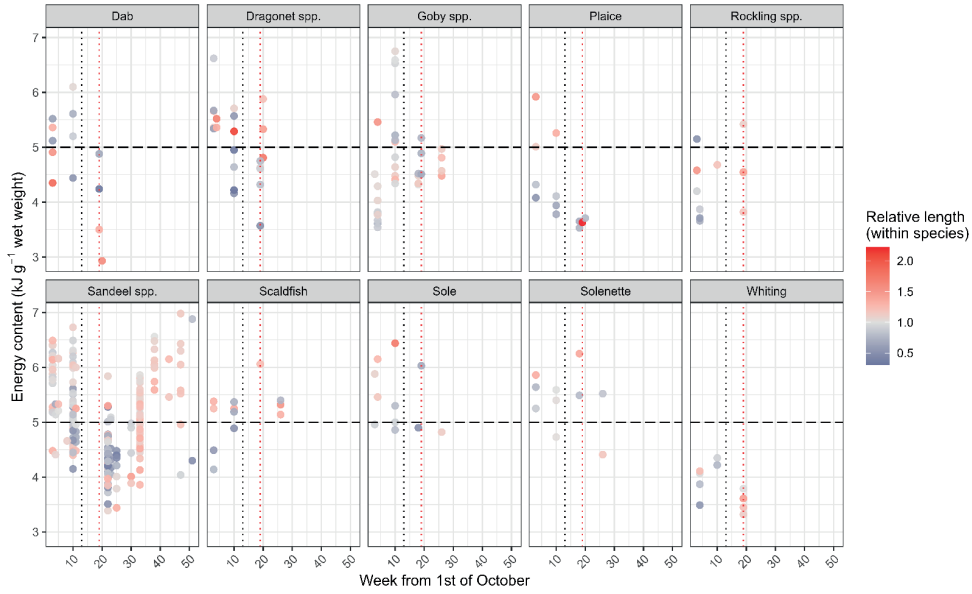
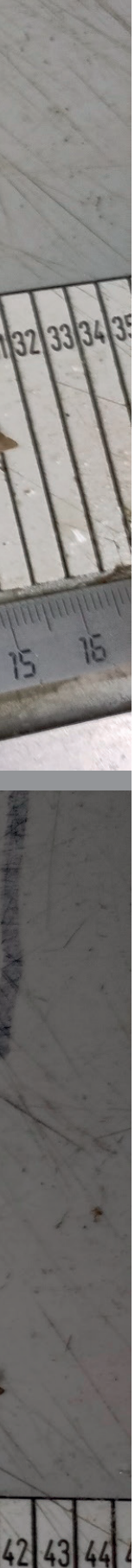


Figure S9: Energy content (kJ g^{-1} wet weight) per species, coloured by relative length (i.e., individual length relative to the mean length within each species).


4 5 6 7 8 9
10 11 12 13 14


1 2 1 3 1 4
14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41



4

Rapid identification methods for the three most abundant sandeel (Ammodytidae) species in the southern North Sea

Bram Parmentier, Judith van Bleijswijk, Eva Immler, Maartje Brouwer, Harry Witte, Bram Couperus, Geert Aarts, and Rob Witbaard

ABSTRACT

Sandeels are abundant, small and elongated fish species on the continental shelves of the northern hemisphere and key players in marine food webs. They contribute significantly to the total fish biomass and are an important food source for many piscivorous fish, seabirds and marine mammals. In the southern North Sea, three relatively abundant and closely related sandeel species can be found: the Lesser sandeel *Ammodytes marinus*, the Small sandeel *Ammodytes tobianus* and the Greater sandeel *Hyperoplus lanceolatus*. Morphological identification of these species is often challenging and time-consuming, and impossible for severely damaged individuals. Yet accurate species determination is essential for understanding their species-specific ecological roles, including habitat use, distribution patterns, and spawning periods. Knowledge of these factors on the species level is especially important in the North Sea where large-scale human activities such as fisheries, sand extractions, and the construction of offshore wind farms, may affect sandeel habitat and abundance. To improve the species identification, we developed a cheap, easy and rapid molecular screening method for the three most abundant sandeel species in the southern North Sea. We present three diagnostic primer pairs and a Real-time PCR strategy to identify specimens of *A. marinus*, *A. tobianus* and *H. lanceolatus* and provide suggestions for the use of easy to score reliable morphological characteristics. Results of Real-time PCR and morphological identification were compared, and both methods were validated by Sanger sequencing of sandeel individuals. An additional proof of concept is presented for cheap and simple MinION sequencing of sandeel specimens.

INTRODUCTION

Sandeels (family Ammodytidae) are small, elongated fishes that can be highly abundant (Chapter 2). For example, in the North Sea, they contribute 15–25% of total fish biomass (Christensen et al., 2013; Sparholt, 1990), and up to 24% of environmental DNA in marine samples (van Bleijswijk et al., 2020). Their high abundance, high energy content, and dual benthic and pelagic occurrence make them an important food source for many piscivorous fish, seabirds, and marine mammals (Engelhard et al., 2014; Régnier et al., 2024). In addition to their ecological importance, sandeels are also heavily exploited by humans for industrial use (Han et al., 2012; ICES, 2024a).

The Ammodytidae family comprises seven genera and 34 species (Froese & Pauly 2025), some of which are morphologically so similar that species identification based on morphological traits can be challenging (Nævdal & Thorkildsen 2002, Heessen et al. 2015). Correct identification at the species-level is a prerequisite for understanding their species-specific ecological niches and roles, including habitat use, distribution patterns, and spawning periods. Such knowledge at the species-level is important for effective fisheries management and conservation, particularly in the southern North Sea. In this region, large-scale human activities such as fishing, sand extraction (Witbaard et al., 2025), construction and operation of wind farms (Cresci et al., 2022; van Deurs et al., 2012), and anthropogenic noise (Carlson et al., 2025) may affect sandeels by altering their abundance, condition, behaviour, and habitats, thereby influencing the wider marine ecosystem through their key role in the food web.

In the Dutch coastal North Sea, the three most abundant species are: the Lesser sandeel *Ammodytes marinus*, the Small sandeel *Ammodytes tobianus* and the Greater sandeel *Hyperoplus lanceolatus* (Tien et al., 2017; van Hal et al., 2021). Although *A. marinus* is also referred to as "Raitt's sandeel" (e.g. Wright et al. 2017), and *A. tobianus* as the "lesser sandeel" (e.g. Behrens & Steffensen, 2007), we adopt the former names, following Fishbase (Froese & Pauly 2026). Two other North Sea species, Corbin's sandeel *Hyperoplus immaculatus* and Smooth sandeel *Gymnammodytes semisquamatus*, are only occasionally observed along the Dutch coast (Heessen et al., 2015). While the three abundant species along the Dutch coast can be distinguished based on morphological characteristics (Macer, 1966; Reay, 1970; van Deurs et al., 2012; Thiel & Knebelsberger, 2016), accurate morphological identification is challenging, especially to distinguish *A. marinus* and *A. tobianus* (Nævdal & Thorkildsen 2002; Heessen et al. 2015). Although adult *H. lanceolatus* can be distinguished from *A. marinus* and *A. tobianus* based on its size, juveniles of *H. lanceolatus* can be easily

overlooked because, unlike adults, their size is not a reliable first indicator for identification, requiring careful examination of morphological features. Additionally, sandeels collected with bottom dredges are often damaged or missing body parts which are essential for identification. In such cases, morphological species identification is practically impossible.

DNA sequencing provides a reliable alternative for species identification (Costa et al., 2012; Knebelsberger et al., 2014; Thiel & Knebelsberger, 2016). Thiel & Knebelsberger (2016) report diagnostic characters in the mitochondrial cytochrome-c-oxydase subunit I (COI) gene for *A. marinus* and *H. immaculatus* but not for *A. tobianus* and *H. lanceolatus*, whereas the nuclear Rhodopsin gene contained diagnostic characters for *H. lanceolatus*. A drawback of DNA sequencing is that it requires several steps (PCR, library preparation and sequencing) and can be costly. Therefore, we aimed to develop a cheap, rapid, reliable, and easy-to-apply screening method for the three most abundant sandeel species occurring in the Dutch part of the North Sea. In this paper, we describe three diagnostic primer pairs and a real-time PCR strategy to identify *A. marinus*, *A. tobianus*, and *H. lanceolatus*. We also evaluate species identifications based on morphological characteristics. In addition, we present the results of a small test using ONT flongle flow cell sequencing of the COI and rhodopsin genes as a proof of concept for relatively cheap and fast in-house sequencing of sandeel specimens.

MATERIAL AND METHODS

Sandeel collection

Sandeels analysed in this study originated from three different sources: (1) the NIOZ deep-digging dredge surveys (Triple-D; Chapter 2), (2) the annual Dutch shellfish survey (Troost et al., 2024), and (3) water column sampling in the Wadden Sea using a stow net (Maathuis, et al., 2025b). Exact sampling locations are shown in Figure S1. After collecting, sandeels were stored in plastic bags and frozen at -20°C.

DNA extraction

In the laboratory, two pieces of muscle tissue were taken from the inner dorsal side of each sandeel specimen using sterile (flamed) scalpels. Sampling the inner tissue avoided potential cross-contamination among specimens due to skin contact during catch or storage. The muscle tissues were placed individually in sterile 1.5 ml Eppendorf tubes on ice and stored at -20 °C until DNA extraction. DNA extractions were done in a decontaminated workstation

(10 min UV exposure and 10% bleach) inside a pre-PCR laboratory with over pressured HEPA filtered air inlet. To reduce costs, we used a Rapid Simple Alkaline Extraction (Rudbeck and Dissing 1998): muscle tissues were incubated for 30 min, in 20 µl 0.2 M NaOH in a thermomixer at 75°C with frequent stirring (2000 rpm 30 sec every 5 min); alkaline lyses was stopped by adding 180 µl 0.04 M Tris-HCl with pH 7.5; Cell debris was spun down for 1 min at 6500 rpm in an Eppendorf centrifuge, and 100 µl of the supernatant (crude lysate) was transferred to a new clean sterile Eppendorf tube prefilled with 200 µl 1xTris buffer to dilute the concentration of co-extracted inhibitors. The resulting solution is referred to as the fish tissue lysate. With each extraction series (typically 24 or 40 samples), we took along one extraction control consisting of a tube without muscle tissue to test the purity of the extraction reagents and to test for cross-contamination among samples during the extraction procedure. The tissue lysates were used within 4 hours for the Real-time PCR runs. Additionally, for a subset of specimens, the same lysates were used to generate larger amplicons for Sanger sequencing (for validation of the real-time PCR results).

Design of diagnostic primer sets

To distinguish the three sandeel species, we designed diagnostic primers based on available reference sequences: Reference sequences (n=34) of the rhodopsin gene of four sandeel species *A. marinus*, *A. tobianus*, *H. immaculatus*, and *H. lanceolatus* and an outgroup of the sand goby *Pomatoschistus* minutes were analysed with the software package ARB (Ludwig et al. 2004; see distance tree in Figure S2). A larger number of reference sequences (n=95) covering eight sandeel species, were available for the mitochondrial COI gene (see distance tree in Figure S3). Species-specific primers were developed using the ARB tool "Design probes". Potential primer sequences were evaluated in the alignment mode according to the requirements: no mismatches with target species, and at least 1 mismatch in the final character at the 3' primer side for non-target species. These criteria were met for *H. lanceolatus* (Figure S4), and *A. marinus* (Figure S5), but not for *A. tobianus* (Figure S6). The best we could do here was to design a primer pair that would amplify all *A. tobianus* haplotypes and some *H. lanceolatus* haplotypes. By using the three primers in a set, and comparing results among primers, a correct identification of all three sandeel specimen would still be possible.

Testing diagnostic Real-time PCRs against Sanger sequencing

Real-time PCR master mixes for each of the three sandeel species were prepared by combining 0.6 µL of newly designed diagnostic forward and reverse primers (10 µM) with 10 µL AccuStart II PCR ToughMix© (2×), 0.5 µL EvaGreen,

and 6.8 µL molecular grade water. Preparation was performed manually in a DNA-free clean laboratory with over-pressured HEPA-filtered air, using only sterile commercially purchased or UV-sterilized consumables. In another pre-PCR lab, the three mixes (one per primer pair) were distributed over 96 well Real-time PCR plates by a pipetting robot (Opentrons OT-2). Subsequently, the robot added 1.5 µls of fish tissue lysate to each well with 18.5µl of diagnostic master mix, such that the lysate of one specimen was added to all three master mixes. Finally, the plates were sealed with optical seal and transferred to Real-time PCR machines (Biorad CFX and CFX OPUS). Cycler programmes consisted of an initial denaturation for 3 minutes at 94 °C, then 37 cycles of 30s at 94°C, 15s annealing at a temperature depending on the diagnostic primer pair, 60s extension at 72°C, and finishing with 5 min at 72°C, a cool down of 5 min at 4°C and a hold at 18°C.

The Real-time PCR results were validated using Sanger sequencing. Both the mitochondrial cytochrome oxidase subunit I (COI) gene and the nuclear rhodopsin gene were sequenced, as these contain diagnostic sites for *A. marinus* and *H. lanceolatus* (Thiel and Knebelsberger 2016). Partial sequences (~650 nucleotides) of the COI gene were obtained with primers Fish-BCL 5′-TCAACYAATCAYAAAGATATYGGCAC-3′ and Fish-BCH 5′-ACTTCYGGGTGRCCRAARAATCA-3′ (Baldwin et al., 2009; Becker et al., 2011). Partial sequences (~464 nucleotides) of the rhodopsin gene were obtained using the primers Rh545 (5′-GCAAGCCCATCAGCAACTTCCG-3′) and Rh1039r (5′-TGCTTGTTCATGCAGATGTAGA-3′) developed by Chen et al. (2003). The PCR reaction mixture contained 25µL AccuStart II PCR ToughMIx(2x), 1.5 µL of both primers (10µM), 20 µL molecular grade water, and 2 µL fish tissue lysate. After an initial denaturation for 3 minutes at 94 °C, thermal cycling was performed with 36 cycles of 30s at 94°C, 15s annealing at 56°C, and 60s extension at 72°C, followed by a final extension of 5 min at 72°C, cool down of 5 min at 4°C and a hold at 18°C. Subsamples of all PCR products were visualized on a 2% agarose gel. Products were purified and sequenced by BaseClear (Leiden, Netherlands). The first set of 17 specimens were sequenced in two directions, aligned, and trimmed using Chromas Pro. After evaluating the location of the diagnostic sites in the rhodopsin and COI gene amplicons, the remaining 111 samples were sequenced one way, with only the forward primers for each of the genes.

For the diagnostic Real-time PCR performance test, the initial set of newly designed primer pairs (Table 1, set 1 with primer pairs 1, 2 and 3ini) was used together with negative controls. Comparison of the results with Sanger sequencing (Figure S7) revealed that the primer pair 3ini was not specific for *A. tobianus* but also amplified the two other species. To fix this problem, we ad-

opted a mismatch amplification primer design according to Morita et al. (2008) for discrimination among very closely related species: with 1 primer mismatch in the second last character at the 3' side for the target species, and 2 primer mismatches at the two last characters for non-target species. A second batch of sandeel specimens were tested with the updated primer pairs (Table 1, set 2, primer pairs 1, 2 and 3) using a convenient similar annealing temperature Ta of 63°C for all three primer pairs. The results of this second test (Figure S8) revealed a reduced specificity of primer pair 2, leading to poor diagnostics of *H. lanceolatus*. The third configuration (Table 1, set 3) consisted of two Real-time PCR runs: one run with Ta 63°C using primer pairs 1 and 3 (for *A. marinus* and *A. tobianus* respectively) on one plate, and a second run with Ta 67°C for primer pair 2 (for *H. lanceolatus*). Figure 1 shows geographic locations for the samples that were analysed by Real-time PCR with this primer set 3, and for the selection of these samples that was also Sanger sequenced.

Table 1: Primer pairs used for screening individual sandeel species *A. marinus* (Amar), *A. tobianus* (Atob) and *H. lanceolatus* (Hlan) based on cytochrome-c-oxydase subunit I (COI) and rhodopsin (Rho) gene sequences. "F" or "R" in the primer names indicates whether the primer is forward or reverse. Primer pair 3 forward is a mismatch primer, as indicated by "MM" in the primer name.

				Ta (°C)		
Primer pair	**Primer name**	**Sequence 5'-3'**	**Reference**	Set 1	Set 2	Set 3
1	Amar_COI_F	GCCCCTGACATAGCATTT	this study	63.0	63.0	63.0
	Amar_COI_R	TGAAGAAATCCCGGCTAG	this study			
2	Hlan_Rho_F	GTGCCCCCTCTTGTCGGT	this study	67.0	63.0	67.0
	Hlan_Rh1039_R	TGCTTGTTCATGCAGATGTAGA	Chen et al. (2003)			
3ini	Atob_Hlan_COI_F1	ATCAACTTCATCACCACG	this study	57.5	-	-
	Atob_Hlan_COI_R1	GTCTGTAAGAAGCATTGTG	this study			
3	Atob_Hlan_COI_MM_F2	GCAATCAACTTCATCACCATG	this study	-	63.0	63.0
	Atob_Hlan_COI_R2	GGTCTGTAAGAAGCATTGTG	this study			

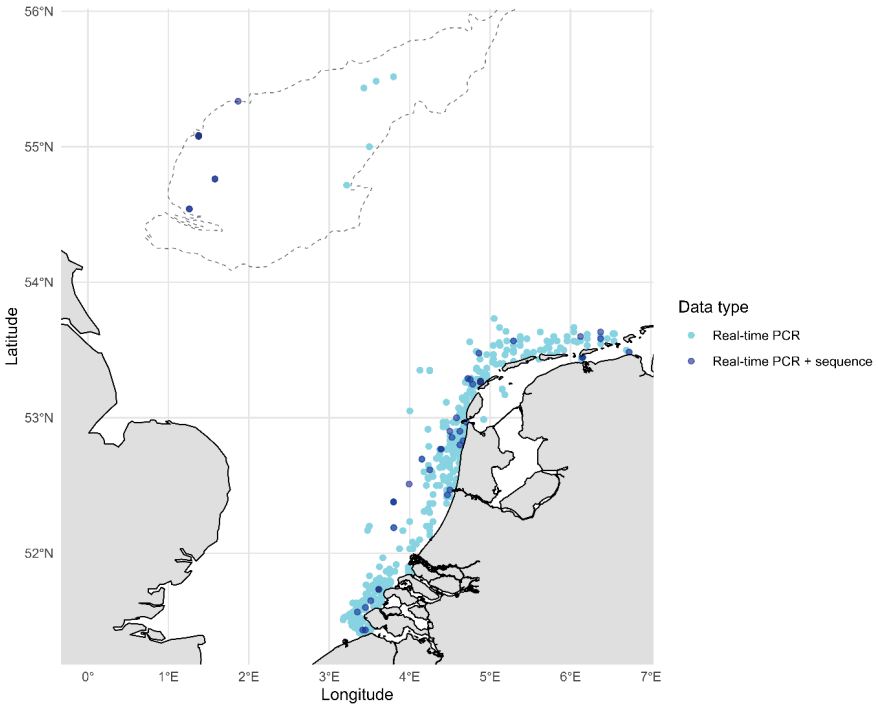


Figure 1: Map of sampling locations of sandeels analysed with primer set 3, indicating individuals used for Real-time PCR only (n = 703) and those also analysed by Sanger sequencing (n = 50).

Morphological identification

For a subset of DNA-identified sandeel specimens (based on Sanger sequencing, Real-time PCRs with primer set 3, or reliable identifications with primer set 2; Figure S9; Table 2), we evaluated detailed morphological identification to distinguish *A. marinus*, *A. tobianus*, and *H. lanceolatus.* A two-step method was used: In the first step, premaxillae protrusibility, the presence of two vomerine teeth, a dark spot on the snout, and the relative length of the pectoral fin were used for distinguishing the genera *Hyperoplus* and *Ammodytes*. In the second step, pigmentation at the base of the caudal fin, the M-shaped band at the base of the caudal fin, general body colour, and the number of dorsal-fin rays, differentiated between *A. marinus* and *A. tobianus* (van Deurs et al. 2012, Thiel and Knebelsberger 2016).

Based on this evaluation, we selected fast-to-score morphological traits that were found to be useful for distinguishing sandeel species in large numbers. These traits were then used to identify sandeels collected during the annual Dutch shellfish survey (Troost et al., 2024). A subset of these sandeels was iden-

tified using the above-described DNA methods (Sanger sequencing and Real-time PCR results with primer set 3, Table 2) and thus provides insights into the accuracy of "fast" morphological identification for large sample sizes. We also examined whether identification accuracy was related to fish length or physical damage.

Table 2: Overview of DNA-based identification methods used to validate morphology-based species identifications.

DNA-based identification	Primer set	Morphology detailed	Morphology fast
Real-time PCR	1	0	0
Real-time PCR	2	44	0
Real-time PCR	3	52	354
Sanger sequencing	-	27	16

RESULTS

Validating diagnostic Real-time PCR

Crude lysates of dorsal muscle tissues of 46 sandeel specimens collected from various southern North Sea locations (Figure 1) were analysed using Real-time PCR runs with the best performing newly developed primer set (Table 2, set 3). Species identity was assigned based on the lowest threshold cycle (Cq) values across the three separate PCR reactions (Figure 2). For 42 specimens (9 *A. tobianus*. 30 *A. marinus*, 3 *H. lanceolatus*), the lowest Cq values were consistent with the Sanger sequencing results. Four specimens produced no signal (Cq > 37) and were afterwards identified by Sanger sequencing as *Gymnammodytes semisquamatus* (not a target species in our primer design). In addition to these 46 specimens, eight other sandeel samples are not shown in Figure 2 because they either failed to amplify with the PCR primers (n = 4) or produced unreadable sequences (n = 4).

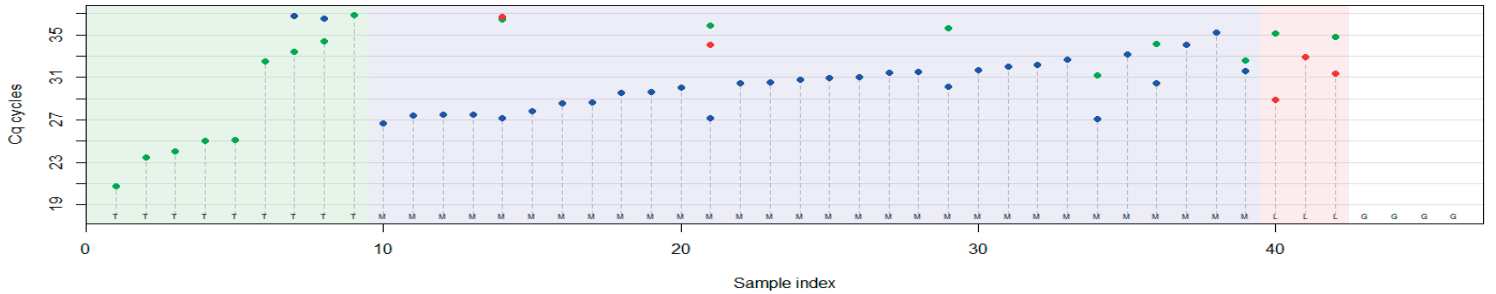


Figure 2: Validation of Real-time PCR: Cq values of tissue lysates of sandeel specimens using diagnostic primer pairs for *A. marinus* (pair 1, blue dots), for *H. lanceolatus* (pair 2, red dots) and for *A. tobianus* and some *H. lanceolatus* genotypes (pair 3, green dots). Capital letters along the x-axis indicate the results of Sanger sequencing (T=*A.tobianus*; M=*A.marinus*; L=*H.lanceolatus*; G=*Gymnammodytes semisquamatus*). Per sandeel species, individuals are arranged from left to right according to the difference between the lowest Cq and the second lowest Cq of the three primer pairs. Background colours correspond to the diagnostic primer pair with the lowest Cq. If a second primer did not amplify, that Cq value was set to 37 cycles (cut-off point).

Application of diagnostic tests to large amounts of field sandeels

After the successful validation of the PCR method with the sanger sequencing on basis of 46 sandeel specimens (Figure 2) we were confident that the used primer sets were sufficiently accurate for genetic identification of high numbers of field samples. So, next we used a large set (757) of specimens which were identified on basis of morphology and which were also collected in the southern North Sea (including the Dogger Bank and Wadden Sea) during the years 2019 to 2023. The morphological identification of these specimens was reassessed by using the newly developed Real-time PCR assays. The results showed that 85% of the PCR assays successfully assigned sandeel tissue to a species. 11% of the specimens (82 individuals) did not yield a real-time PCR signal with any of the three primer pairs and were therefore not included in Figure 3. For the remaining 4% of the specimens (28 individuals), the difference in Cq values between the two lowest Cq values of the three primer pairs was less than 0.5, including measurements with Cq values above 36.5. Such identifications were considered less reliable, and no species assignment was made. Those unassigned specimens are shown with a white background in Figure 3 and were excluded from further evaluation of morphological species identification in Section 3.3.

Evaluation of morphological traits in genetically determined sandeel species

We used a two-step approach to separate the three sandeel species on basis of morphological characteristics. The first step is used to distinguish *Ammodytes* from *H. lanceolatus*. As shown in Table 3, premaxillae protrusibility and vomerine teeth were generally consistent with known species-specific characteristics (indicated with the asterisk). In contrast, the dark spot on the snout which is remarked as a unique characteristic of *H. lanceolatus* was also frequently observed in *A. marinus*. This makes it an unreliable trait for distinguishing these two genera. Another distinguishing character used is the relative length of the pectoral fin. In general, this length was smaller in *H. lanceolatus* than in the *Ammodytes* species, although some overlap between the genera was observed (Figure S10). Therefore, only individuals with a pectoral fin length of less than 6% of total body length can be confidently identified as *H. lanceolatus*.

In the second step, *Ammodytes* species can be distinguished based on caudal fin characteristics, body colour, and the number of dorsal-fin rays. In our study, the M-shaped band at the base of the caudal fin proved to be a more reliable characteristic than caudal fin pigmentation (Table 3). Body colour was not informative, as *A. marinus* exhibited both colour patterns in nearly equal numbers. Although the mean number of dorsal-fin rays differed slightly between species,

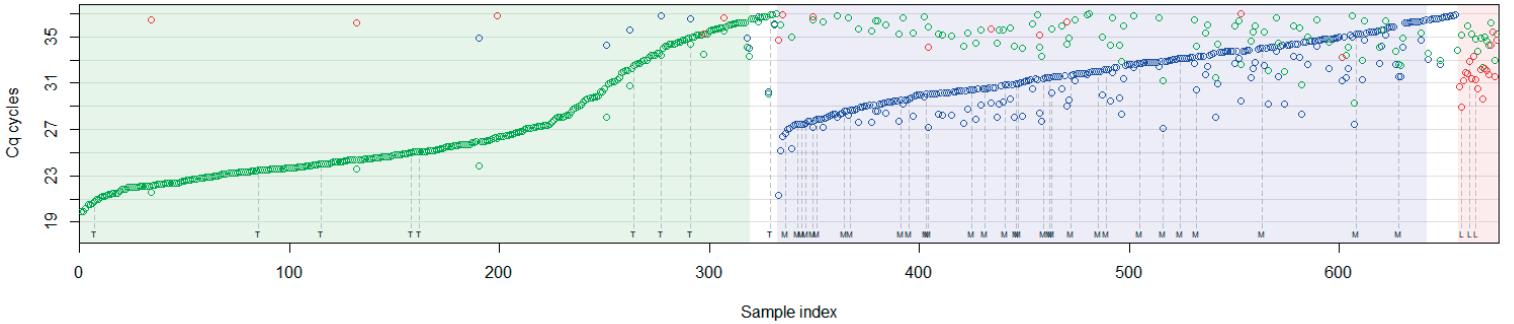


Figure 3: Real-time PCR results of 675 sandeel specimens: Cq values of tissue lysates of sandeel specimens using diagnostic primer pairs for *A. tobianus* and some *H. lanceolatus* genotypes (green dots), for *A. marinus* (blue dots), and for *H. lanceolatus* (red dots). Per sandeel species, specimens are arranged from left to right according to the difference between the lowest Cq and the second lowest Cq. If a second primer did not amplify, that Cq value was set to 37 cycles (cut-off point). Background colours correspond to the primer pair with the lowest Cq. Where the difference in Cq was less than 0.5 cycles, the background colour was set to white, indicating an area of uncertainty. Capital letters along the x-axis indicate the results of Sanger sequencing (T=*A.tobianus*; M=*A.marinus*; L=*H.lanceolatus*).

the overlapping ranges and standard deviations indicate that this trait is not useful for reliably separating *A. marinus* and *A. tobianus* (see Figure S10).

Based on this evaluation of detailed morphological traits, we conclude that premaxillae protrusibility and the presence of vomerine teeth are suitable characteristics for distinguishing *H. lanceolatus* from *Ammodytes.* The relative length of the pectoral fin may serve as an additional indicator, however, we found it too time-consuming to measure in large sample sizes. Within the *Ammodytes* species, the M-shaped band at the base of the caudal fin proved to be a suitable characteristic for species identification in large numbers of sandeels. These characteristics were considered suitable for a rapid morphology-based identification approach because they are (relatively) easy to score and can be assessed efficiently for large numbers of specimens.

Table 3: Observed detailed morphological traits (two-step method) for sandeel species, identified by real-time PCR or DNA sequencing. Numbers indicate the number of specimens assessed. Asterisks (*) denote traits that were correctly observed in accordance with the genetically confirmed species identity. For numerical traits, the range, median, standard deviation (SD), and sample size are provided. General body colour is classified as green–blue (GB) or yellow–green (YG).

Morph. Step	Characteristic	*A. marinus*			*A. tobianus*			*H. lanceolatus*		
		present	**absent**	**unclear**	**present**	**absent**	**unclear**	**present**	**absent**	**unclear**
1	Premaxillae protrusible	47*	5	5	33*	1	0	3	14*	0
1	Two vomerine teeth present	0	52*	5	0	34*	0	15*	1	1
1	Dark spot nose	27	28*	2	2	32*	0	16*	1	0
1	Number of dorsal-fin rays	41-59; 56 ± 3.3 (46)			49-58; 52 ± 2.1 (31)			50-56; 53.5 ± 1.9 (14)		
2	Pigmentation at base of caudal fin	54*	3	0	8	25*	1	7	10	0
2	M band at the base of caudal fin	2	54*	1	32*	2	0	6	11	0
2	General body colour	GB (26)* YG (26)			GB (5) YG (28)*			GB (7) YG (10)		
2	Relative length of pectoral fin	6.4-11.7; 9.4 ± 1.0 (42)			7.4-10.8; 9.4 ± 0.8 (29)			5.2-9.8; 6.8 ± 1.1 (16)		

Reliability of easy to score morphological traits for large sample sizes

Morphological identification of *A. marinus* was highly accurate, with 97% of individuals correctly classified, whereas identification of *A. tobianus* was less accurate, with 77% correctly classified when compared to DNA identification (Table 4). Surprisingly, misidentifications were not necessarily linked to damaged individuals. Identification errors also occurred more frequent for large (≥10 cm) than for small (<10 cm) individuals (Table 5). Using easily scored morphological traits, it was not possible to identify all specimens to the species level. Consequently, some individuals were assigned only to the genus *Ammodytes* (Table 4). Due to the low number of encounters, *Hyperoplus lanceolatus* was not assessed in detail. Nevertheless, only one specimen that had been morphologically identified as *Ammodytes* was found to possess the *H. lanceolatus* genotype, indicating that genus-level identification based on morphology using the two-step method is largely reliable.

Table 4: Effect of sandeel damage on successful morphological identifications, as evaluated with DNA-based identification results. Numbers in the columns indicate the number of specimens.

Morphological Identification		**DNA identification**				
		A. marinus	***A. tobianus***	***H. lanceolatus***	**Total**	**Correct %**
A. marinus	No damage	32	1	0	33	97
	Damaged	5	0	0	5	100
	Total	**37**	**1**	**0**	**38**	**97**
A. tobianus	No damage	4	14	0	18	78
	Damaged	1	3	0	4	75
	Total	**5**	**17**	**0**	**22**	**77**
Ammodytes	No damage	18	12	0	30	100
	Damaged	5	7	0	12	100
	Only head	79	119	1	199	100
	Total	**102**	**138**	**1**	**241**	**100**

Table 5: Effect of sandeel length (Small <10 cm, Large ≥10 cm) on correct morphological identifications as evaluated with DNA-based identification results. Numbers in the columns indicate the number of specimens.

Morphological Identification	DNA identification					
	Length	***A. marinus***	***A. tobianus***	***H. lanceolatus***	**Total**	**Correct %**
A. marinus	Small	15	1	0	16	94
	Large	22	0	0	22	100
	total	**37**	**1**	**0**	**38**	**97**
A. tobianus	Small	0	10	0	10	100
	Large	5	7	0	12	58
	Total	**5**	**17**	**0**	**22**	**77**
Ammodytes	Small	6	18	0	24	100
	Large	17	1	0	18	100
	total	**23**	**19**	**0**	**42**	**100**

DISCUSSION

We developed a rapid screening method to identify the three most abundant sandeel species (*A. marinus*, *A. tobianus*, and *H. lanceolatus*) in the Dutch coastal zone and southern North Sea. The two co-occurring *Ammodytes* species are morphologically difficult to distinguish, while species specific knowledge is essential to understand their habitat use and the niche they occupy. In our study, we found that commonly used morphological traits are not always easy to observe, which can lead to incorrect species identifications. Moreover, sandeel specimens collected with bottom dredges are often cut in two, leaving only the head or tail. As a result, morphological identification is impossible. These challenges highlight the value of DNA-based approaches for accurate species determination.

The screening method (with diagnostic primer set 3, Table 2) developed in this study proved to be reliable, as Sanger sequencing results were always consistent with the Real-time PCR results. Therefore, this Real-time PCR method provides an accurate approach for species identification of these three sandeel species which co-occur in the coastal southern North Sea. Of the 757 sandeel specimens analysed, including some stored for up to 3 years, approximately 11% did not produce a Real-time PCR signal for any of the primers and could therefore not be assigned to a species. Repeating the extraction and Real-time PCR still did not provide a signal for 61% (25 out of 41) of the sandeel specimen, indicating DNA degradation could be the reason. For ~0.5% of the sandeel (4 specimen caught at Dogger bank) Sanger sequencing revealed a species identity other

than the three target species, namely *Gymnammodytes semisquamatus*. To detect such cases, additional morphological examination or Sanger sequencing is still useful alongside the Real-time PCR technique.

The Real-time PCR method as described in this paper, using a 25µl PCR volume with expensive PCR-ready mix, costs approximately €1.80 per sample. With a reduced PCR volume e.g. to 10 µl, costs could be reduced to €0.72 per sample. Identification via Sanger sequencing requires sequencing two gene amplicons per sample and costs between 9 and 16 euro per sample (single runs in 96 well plate or in tubes by BaseClear, Leiden). This difference in price can be particularly important when large numbers of samples need to be processed, such as those collected for long-term monitoring.

An alternative for Sanger sequencing could be ONT-sequencing with the relatively cheap and portable MinION (Doorenspleet et al. 2025, Malik et al. 2026). However, since the sandeel species only carry 1-3 diagnostic sites within their two barcode amplicons (COI and rhodopsin genes) it was unclear whether ONT sequencing would be suitable for sandeel species identification. Therefore, we set up a small test with COI and rhodopsin gene amplicons of nine sandeel specimen that had been identified with Sanger sequencing (three specimen each of *A. tobianus*, *A. marinus* and *H. lanceolatus*; Supporting Information). Results (Table S1) show that the largest cluster of dereplicated reads always gave an ID% score > 99.695 relative to a reference sequence in the Nt database, and was always correctly assigned to the appropriate species. Consistently, for each specimen, the largest cluster yielded the correct species identification. With a default read quality threshold of 10 (Q10) the largest cluster represented 6-8% of the COI reads and 12-22% of the rhodopsin reads while smaller clusters with lower ID% maximal represented 0.4-0.5% of COI reads and 0.7-1.4% of rhodopsin reads. For reads with a higher quality score (>25), the largest cluster with the highest ID% increased to 29-41% of COI reads and 35-71% of rhodopsin reads (not shown). We estimate that at least 100 specimen samples can be analysed together on a single flongle (small flow cell) that in our test delivered 65 k reads with quality (Q10), corresponding to a sequence cost of about 4 euro per specimen, about half the price of Sanger sequencing, but still 2 times more expensive than the Real-time PCR method. A follow up test should show whether pooling 100 specimen on a flongle will provide 100 correct identifications.

To conclude, accurate identification of sandeel species is essential for understanding their species-specific ecological roles, including habitat use, life-stage-specific distribution patterns (including larval phase), and spawning periods. This species-specific knowledge is crucial for predicting and manag-

ing the potential effects of climate change, anthropogenic stressors, and other environmental changes. Given the key role sandeels play as prey for many predators, such understanding is also fundamental for assessing impacts on the wider marine ecosystem. The rapid, cost-effective, and reliable screening method developed in this study provides a practical solution to the challenges of morphological species identification by enabling accurate, cheap, and quick species-level determination.

Acknowledgements

This work was funded by the Netherlands Organisation for Scientific Research (NWO) through Top Sector Water & Maritime under the project "Forage Fish" (NWOTWM.81.019.008). We thank Jetze van Zwol, Jack Perdon, and the entire crew of the Isis for collecting sandeel during the WOT shellfish survey. We also thank Simon Boon for his extensive laboratory work.

SUPPLEMENT

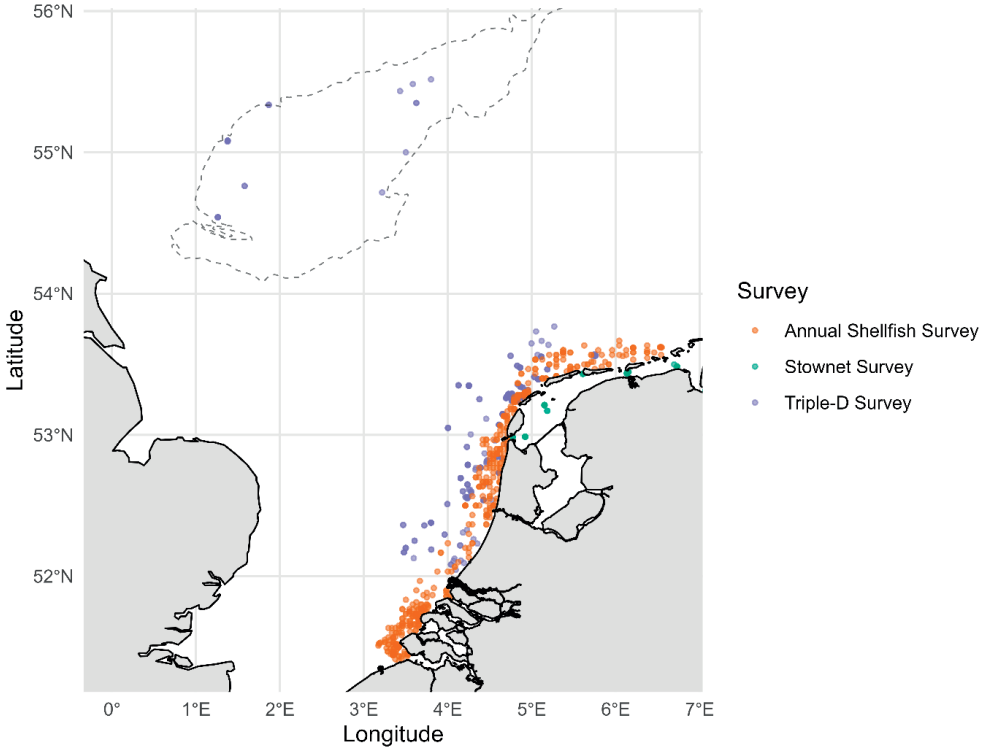


Figure S1: Sample locations of DNA-analysed sandeels, coloured by survey.

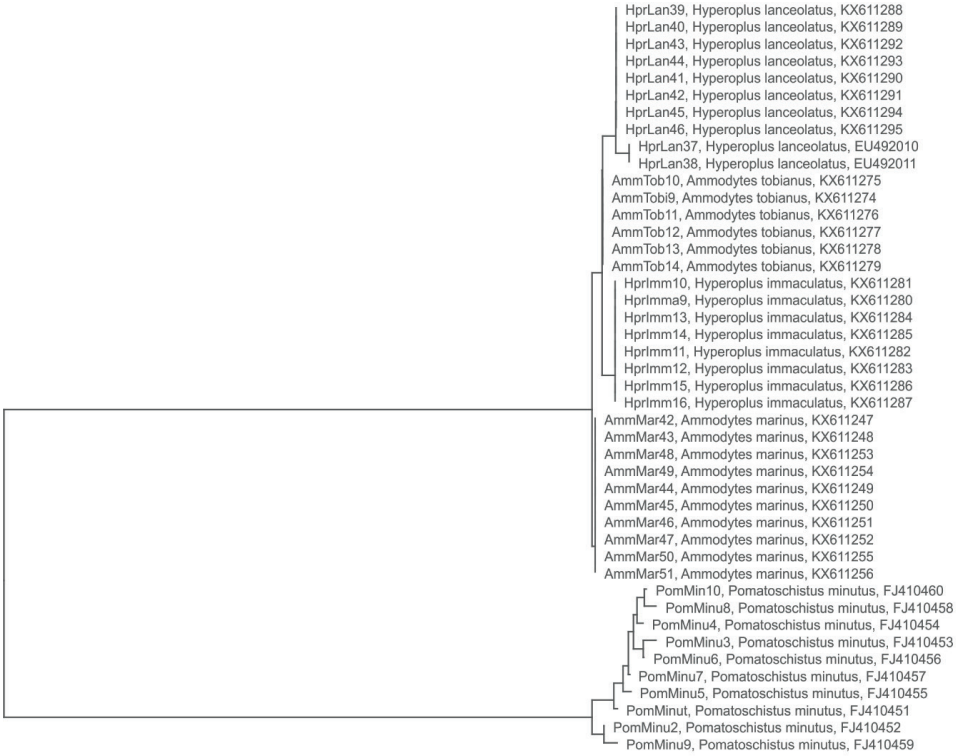


Figure S2: Distance tree of rhodopsin gene sequences of four sandeel species and an outgroup (sand goby), downloaded from GenBank.

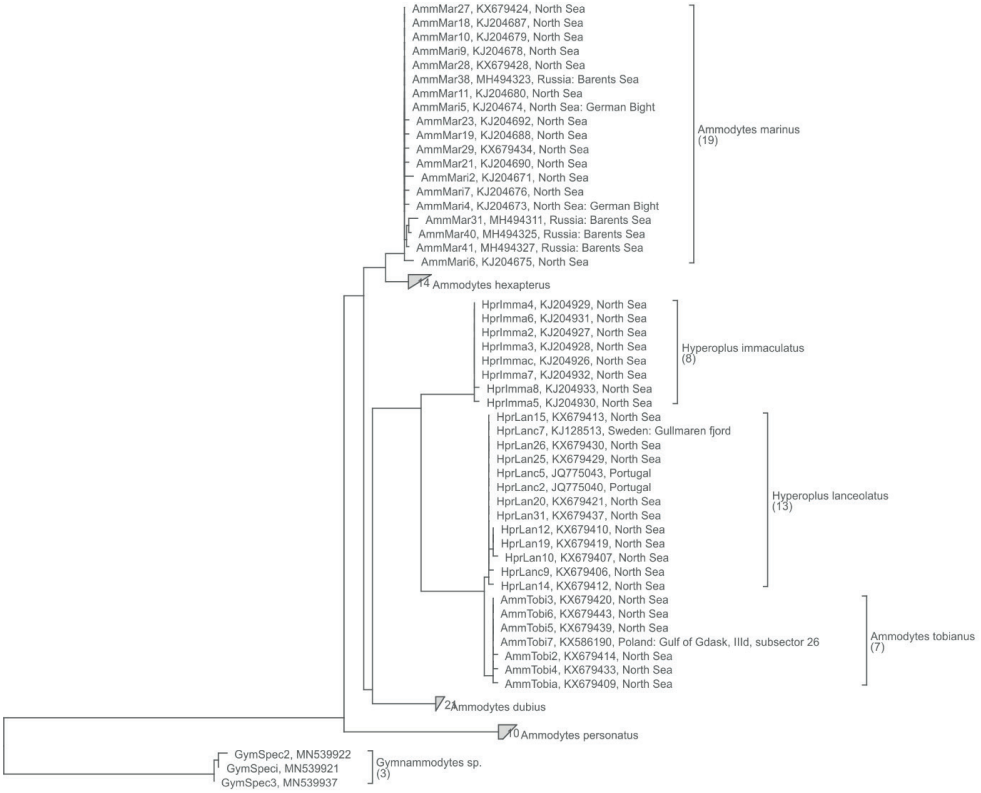


Figure S3: Distance tree of cytochrome-c-oxydase subunit I gene sequences of sandeel species downloaded from GenBank

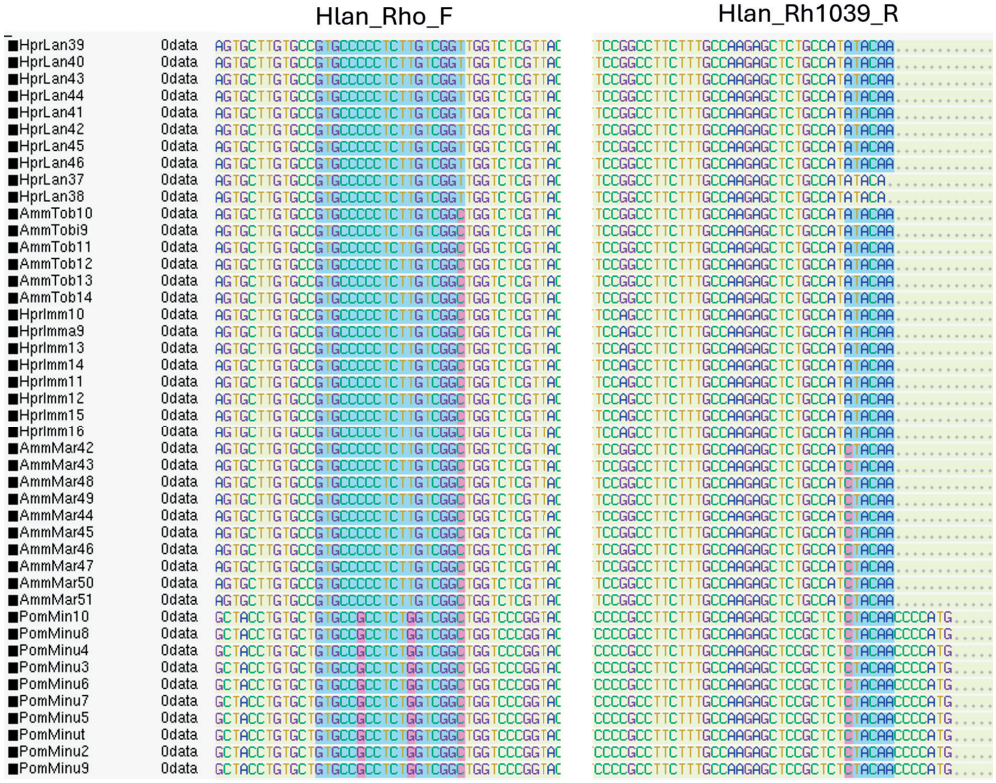


Figure S4: Multiple alignment showing binding regions (blue background) of primers Hlan_Rho_F (5′-GTGCCCCCTCTTGTCGGT-3′) and the first 6 bases at the 3′ side of Hlan_Rh1039_R (5′-TGCTTGTTCATGCAGATGTAGA-3′) of sandeel species *Hyperoplus lanceolatus*, *Ammodytes tobianus*, *Hyperoplus immaculatus*, *Ammodytes marinus* and outgroup *Pomatoschistus minutus.* Mismatches with the primer are indicated with pink backgrounds.

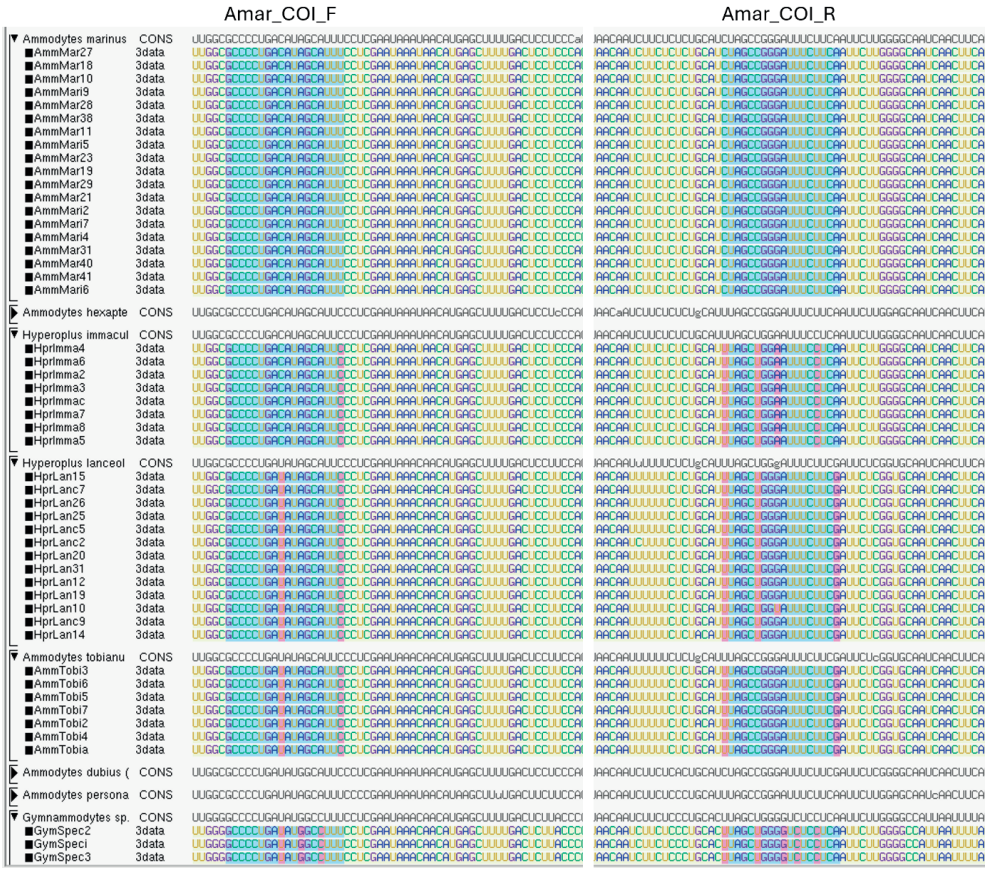


Figure S5: Multiple alignment showing binding regions (blue background) of primers Amar_COI_F (5′-GCCCCTGACATAGCATTT-3′) and Amar_COI_R (5′-TGAAGAAATCC-CGGCTAG-3′) of sandeel species *Ammodytes marinus, Hyperoplus immaculatus, Hyperoplus lanceolatus*, *Ammodytes tobianus*, and Gymnammodytes sp. Mismatches are indicated with pink back grounds.

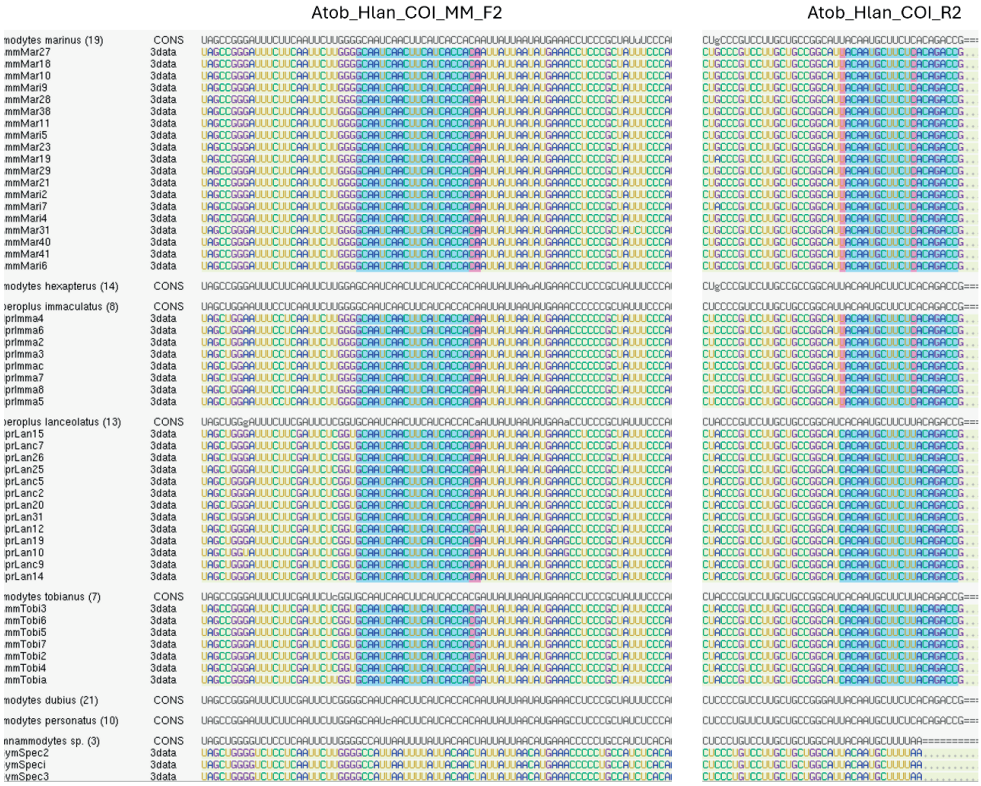


Figure S6: Multiple alignment showing binding regions (blue background) of primers Atob_Hlan_COI_MM_F2 (5′-GCAATCAACTTCATCACCATG-3′) and Atob_Hlan_COI_R2 (5′-GGTCTGTAAGAAGCATTGTG-3′) of sandeel species *Ammodytes marinus, Hyperoplus immaculatus, Hyperoplus lanceolatus*, *Ammodytes tobianus*, and Gymnammodytes sp. Mismatches are indicated with pink backgrounds.

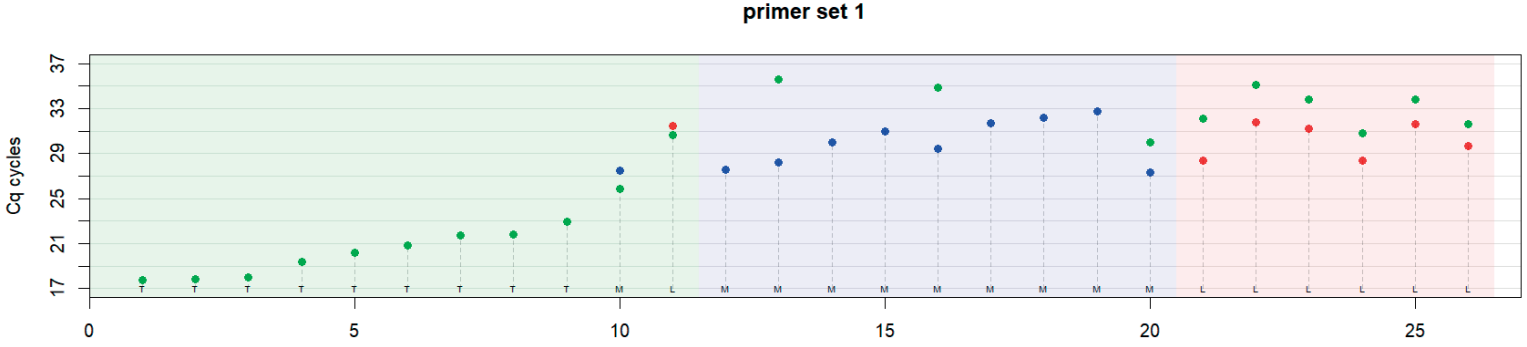


Figure S7: Validation of suboptimal Real-time PCR primer set 1: Cq values of crude lysates of sandeel specimens using diagnostic primer pairs for *A. marinus* (pair 1, blue dots), for *H. lanceolatus* (pair 2, red dots) and for *A. tobianus* and some *H. lanceolatus* genotypes (pair 3ini, green dots). Per sandeel species, individuals are arranged from left to right according to the difference between the lowest Cq and the second lowest Cq of a primer pair. Background colours correspond to the diagnostic primer pair with the lowest Cq. If a second primer did not amplify, that Cq value was set to 37 cycles (cut-off point). Capital letters along the x-axis indicate the results of Sanger sequencing. Primer pair 3ini was not specific enough. This is illustrated by samples 10 and 11, which were identified as *A. marinus* and *H. lanceolatus*, respectively, based on Sanger sequencing.

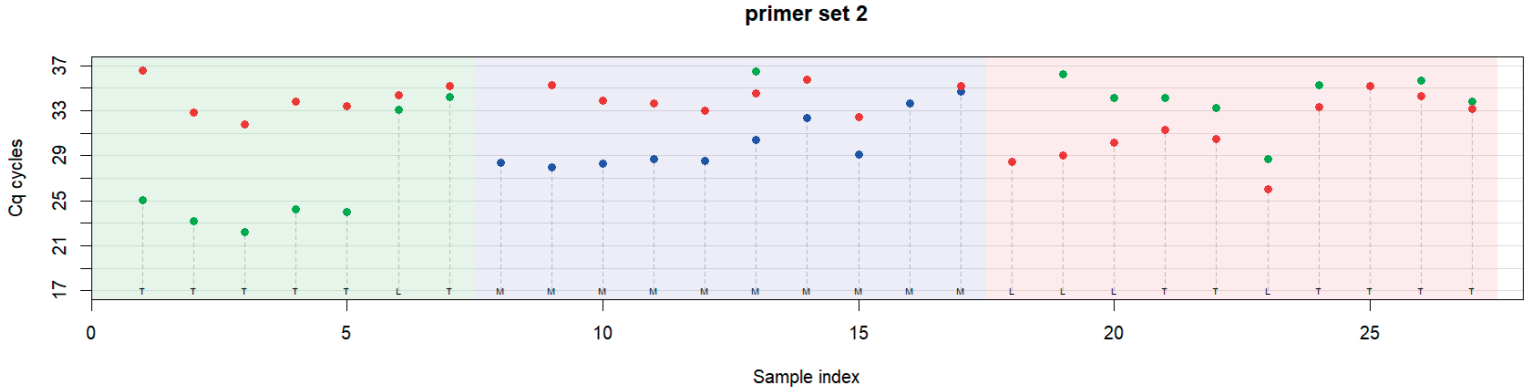


Figure S8: Validation of suboptimal Real-time PCR primer set 2: Cq values of crude lysates of sandeel specimens using diagnostic primer pairs for *A. marinus* (pair 1, blue dots), for *H. lanceolatus* (pair 2, red dots) and for *A. tobianus* and some *H. lanceolatus* genotypes (pair 3, green dots). Per sandeel species, individuals are arranged from left to right according to the difference between the lowest Cq and the second lowest Cq of a primer pair. Background colours correspond to the diagnostic primer pair with the lowest Cq. If a second primer did not amplify, that Cq value was set to 37 cycles (cut-off point). Capital letters along the x-axis indicate the results of Sanger sequencing. The *H. lanceolatus* primer was not specific enough. This is illustrated by samples 21,22, and 24-27, which were identified as *A. tobianus*, based on Sanger sequencing. Sample 6 was also not correctly identified.

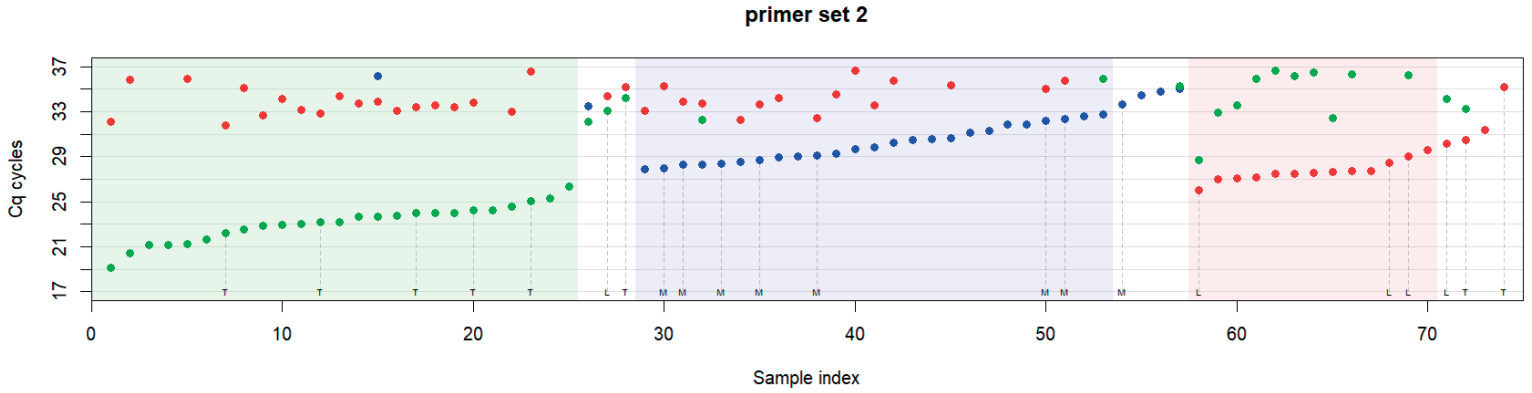


Figure S9: Outcomes of suboptimal PCR primer set 2 used on 74 field specimen: Cq values of crude lysates of sandeel specimens using diagnostic primer pairs for *A. marinus* (pair 1, blue dots), for *H. lanceolatus* (pair 2, red dots) and for *A. tobianus* and some *H. lanceolatus* genotypes (pair 3, green dots). Per sandeel species, individuals are arranged from left to right according to the difference between the lowest Cq and the second lowest Cq of a primer pair. If a second primer did not amplify, that Cq value was set to 37 cycles (cut-off point). Capital letters along the x-axis indicate the results of Sanger sequencing. Background colours correspond to the diagnostic primer pair with the lowest Cq, provided the identification was considered reliable. Reliability was primer-specific: specimens were classified as *A. tobianus* when the corresponding primer amplified first with a Cq value below 27. Specimens were classified as *A. marinus* when amplification occurred first with a Cq value below 33, while specimens were classified as *H. lanceolatus* when amplification occurred first with a Cq value below 30.

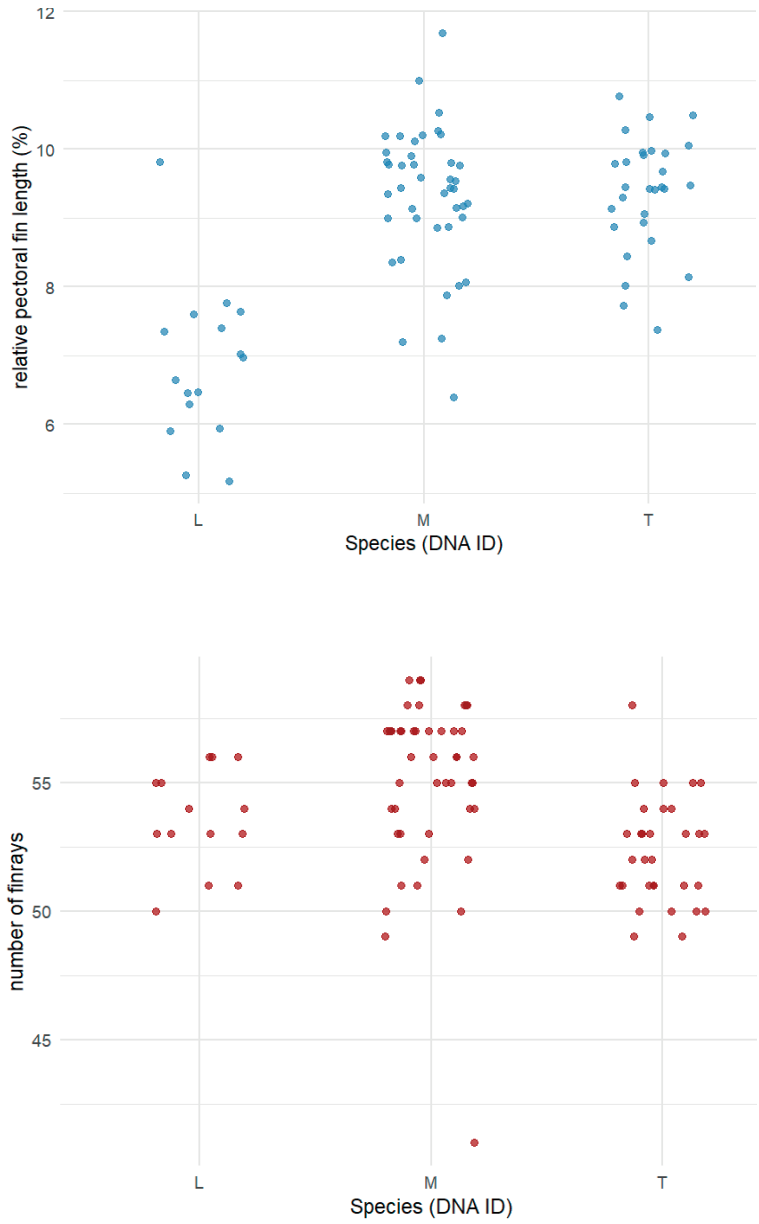


Figure S10: Top: Relative pectoral fin length as a proportion of total body length for each species (DNA-identified). Bottom: Number of dorsal-fin rays per species (DNA-identified).

Supporting Information

ONT sequencing of sandeel specimens

In order to test whether ONT sequencing could be a (cheaper) alternative for Sanger sequencing of closely related sandeel species, we set up a small test for nine sandeel specimen (3 confirmed *A.tobianus*, 3 *A.marinus*, and 3 *H.lanceolatus*). Sequence libraries were prepared for both COI and rhodopsin gene amplicons using two-step PCR reactions. In the first step, amplicons (~650 nucleotides) of the COI gene were obtained with primers Fish-BCL 5′-TCAACYAATCAYAAAGATATYGGCAC-3′ and Fish-BCH 5′-ACTTCYGGGTGRCCRAARAATCA-3′ (Baldwin et al., 2009; Becker et al., 2011), and amplicons (~464 nucleotides) of the rhodopsin gene were obtained using the primers Rh545 (5′-GCAAGCCCATCAGCAACTTCCG-3′) and Rh1039r (5′-TGCTTGTTCATGCAGATGTAGA-3′) developed by Chen et al. (2003). All primers mentioned above were extended at the 5′-side with M13 tails (M13F tail 5′-TGTAAAACGACGGCCAGT-3′ and M13R tail 5′- CAGGAAACAGCTATGACC-3′). The 20ul PCR reaction mixtures contained 1ul DNA extract, 11.2ul water, 4ul Platinum SuperFi buffer, 1.6ul dNTPs, 0.2ul SuperFi enzyme and 1ul of both forward and reverse primers (10µM). After an initial denaturation for 30s at 98 °C, thermal cycling was performed with 15 cycles of 10s at 98°C, 15s annealing at 53°C for COI and 56°C for rhodopsin, followed by 30s extension at 72°C, a final extension of 5 min at 72°C, cool down of 5 min at 4°C, and a hold at 18°C. Subsamples of all PCR products were visualized on a 2% agarose gel. In the second step, 2ul of the PCR products that were generated in the first step were amplified in a 20ul reaction volume (12.2 ul water, 4ul Platinum Superfi I buffer, 1.6 ul dNTPs, 0.2ul SuperFi1 enzyme) with 1ul M13 primers extended with unique Golay barcodes: bcM13F primer (5′-[12nt Golay]- TGTAAAACGACGGCCAG-3′) and bcM13R primer (5′-[12nt Golay]- CAGGAAACAGCTATGAC-3′). Thermal cycling was performed with 15 cycles of 10s at 98°C, 15s annealing at 60°C, and 30s extension at 72°C, followed by a final extension of 5 min at 72°C, cool down of 5 min at 4°C and a hold at 18°C. One negative control (also labelled with unique barcodes) was taken along during both the PCR steps to check for read contamination resulting in 10 samples with COI amplicons and 10 samples with rhodopsin amplicons

Of each barcoded PCR product, 10µl was added to a pool which was further prepared using the kit SQK-LSK114 with the protocol for Ligation sequencing amplicons V14. The resulting library was loaded on a Flongle (FLO-FLG114) and sequenced with MinKNOW version 24.11.8 using Super accurate basecalling v4.3.0 with minimal quality Q scores of respectively 10 and 25. Simple bioinformatic analyses included sample assignment with Cutadapt based on the presence of unique barcodes of both ends of the amplicon, adapter and primer

removal with Vsearch, and taxonomic assignment of reads using Blast (v. 2.12. 0) versus Nucleotide database Nt (15 Feb 2026). Tables SI1 and SI2 show results of ONT-sequencing.

Table S11. Top Blast Nt hits for OTUs (dereplication clusters) of COI amplicons (with Q10 score) of the three sandeel species.

Sanger sequence ID	ONT COI Blast hit	Total ONT COI reads	OTU rank	OTU cluster size	max % ID	%reads max%ID correct species	%reads max%ID other species
A. marinus	A. marinus	1006	0	58	100	6%	0%
A. marinus	A. marinus	1898	0	109	100	6%	0%
A. marinus	A. marinus	2226	0	133	100	6%	0%
A. tobianus	A. tobianus	2883	0	176	100	6%	0%
A. tobianus	A. tobianus	4649	0	312	99.695	7%	0%
A. tobianus	A. tobianus	2463	0	157	99.847	6%	0%
H. lanceolatus	H. lanceolatus	3587	0	240	100	7%	0%
H. lanceolatus	H. lanceolatus	5172	0	401	100	8%	0%
H. lanceolatus	H. lanceolatus	1701	0	107	100	6%	0%
Control		0					

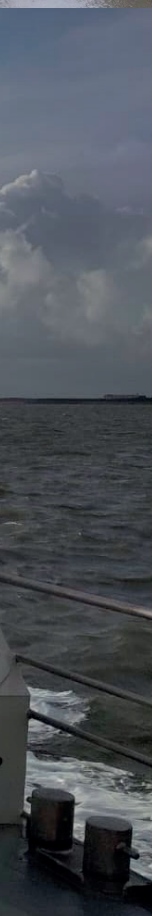
Table S12. Top Blast Nt hits for OTU's (dereplication clusters) of rhodopsin amplicons (with Q10 score) of the three sandeel species.

Sanger sequence ID	ONT Rhodopsin Blast hit	total ONT Rho reads	OTU rank	OTU cluster size	max % ID	%reads 100% ID correct species	%reads 100%ID other species
A. marinus	A. marinus	495	0	65	100	13%	0%
A. marinus	A. marinus	674	0	80	100	12%	0%
A. marinus	A. marinus	554	0	70	100	13%	0%
A. tobianus	A. tobianus	2533	0	513	100	20%	0%
A. tobianus	A. tobianus	3688	0	762	100	21%	0%
A. tobianus	A. tobianus	2183	0	473	100	22%	0%
H. lanceolatus	H. lanceolatus	1946	0	390	100	20%	0%
H. lanceolatus	H. lanceolatus	3042	0	626	100	21%	0%
H. lanceolatus	H. lanceolatus	3878	0	806	100	21%	0%
Control		0					









5

Spatial and temporal niche differentiation of two sympatric sandeel (*Ammodytes*) species

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ABSTRACT

Sandeel (family Ammodytidae) are semi-pelagic fish that play a key role in marine food webs as prey for seabirds, marine mammals, and piscivorous fish. Despite their ecological importance, species-specific spatial and temporal patterns, particularly in areas of geographic overlap, remain poorly understood. We analysed the seabed occurrence of two sandeel species (*Ammodytes marinus* and *A. tobianus*) collected during the annual Dutch shellfish benthic survey in spring (2016–2018, 2020–2022). Niche differentiation was examined in relation to depth, sediment characteristics, bivalves, salinity, and temporal variables (day of year, relative time-of-day). Both species showed an offshore–nearshore segregation, with *A. marinus* dominating offshore and *A. tobianus* in nearshore areas. While depth largely explained this pattern, substantial unexplained variation remained, suggesting that additional drivers influence their spatial segregation. Furthermore, concurrent measurements of bivalve biomass were negatively associated with the abundance of both sandeel species, suggesting that dense bivalve aggregations may hinder burrowing behaviour, or that sandeel and bivalves differ in sediment preference. Areas of co-occurrence were also observed, and both species of sandeel showed similar diurnal patterns, with higher densities in the evening, as well as comparable interannual trends. In conclusion, although generally segregated across the study area, their overlapping distributions, lack of diurnal differentiation, and similar annual trends suggest that these morphologically similar species can coexist locally without complete competitive exclusion. The resulting distribution maps and temporal insights, including diurnal, seasonal, and long-term abundance trends, could contribute to studies of sandeel–predator interactions and improve our understanding of the species-specific roles that sandeel play as forage fish in coastal ecosystems.

1. INTRODUCTION

Sandeel (family Ammodytidae) are small, elongated, semi-pelagic forage fish that are abundant in coastal marine systems. Due to their high abundance and their presence in the sediment and water column, they play a crucial role in marine food webs, serving as essential prey for a variety of top predators, including seabirds, marine mammals, and piscivorous fish (Engelhard et al., 2014; Link & Garrison, 2002; Régnier et al., 2024; Rindorf et al., 2000). Sandeel are not only ecologically important but also support major industrial fisheries (Han et al., 2012; ICES, 2024). The Ammodytidae family comprises seven genera and 34 recognised species (Froese & Pauly, 2025). Despite being genetically distinct, most sandeel species show similarity in morphology, behaviour, and ecology. However, this apparent similarity, and difficulty identifying them to species level in the field, may partly explain the limited research on their life-history and ecological differences.

A key characteristic of sandeel is their semi-pelagic behaviour, with both a diurnal and seasonal component: during the productive spring and summer months, they forage in the water column by day, while at night they burrow in the seabed (Engelhard et al., 2008; Freeman et al., 2004; Henriksen et al., 2021; Winslade, 1974). Outside these months, cold-water sandeel typically overwinter in a dormant state, burrowed in the seabed (van Deurs et al., 2010). This strategy is thought to conserve energy in periods of low food availability, as swimming is costly since they have no swim bladder, and it reduces predation risk during non-feeding periods (Reay, 1970; Wright et al., 2000). When buried, sandeel prefer clean, coarse-grained, silt-poor, and well-oxygenated sandy sediments to ensure sufficient oxygen supply and to avoid clogging of their gills (Holland et al., 2005; Langton et al., 2021; Reay, 1970; Tien et al., 2017; Wright et al., 2000). Furthermore, experimental tests have shown that sediments with a high content (30%) of medium-sized gravel (4–8 mm) are avoided, as it is likely not physically possible for sandeel to bury in excessive gravel (Henriksen et al., 2024). In the water column, sandeel are visual feeders that mainly consume zooplankton such as copepods, but larger species such as *Hyperoplus lanceolatus* also target juvenile fish, including other sandeel species (Macer, 1966; O'Connell & Fives, 1995; van Deurs et al., 2013).

Three sandeel species are commonly found along the Dutch coastal zone: *A. marinus* and *A. tobianus*, and *H. lanceolatus,* though the latter occurs in relatively low numbers (Tien et al., 2017; van Hal et al., 2021) and is therefore not the focus of this study. Among the *Ammodytes* species, *A. marinus* typically occurs at deeper offshore waters (>30 m), while *A. tobianus* is more commonly

found in shallow (<30 m) coastal areas (van Deurs et al., 2012). Although both *Ammodytes* species show a general coastal–offshore separation, their distributions overlap (Tien et al., 2017; van Deurs et al., 2012; van Hal et al., 2021). This overlap suggests that both species partially occupy distinct niches, which allows coexistence in the same habitats. Differences in resource use or prey selection, a key aspect of niche differentiation, have been reported for the two *Ammodytes* species (Macer, 1966). However, Macer's analyses were based on fish from different locations (inshore vs. offshore), so the observed differences likely reflected habitat-based variation rather than true species-specific dietary preferences when the same prey is available. Likewise, potential differences in behaviour, phenology, habitat use, life history, morphology, physiology, and ecological interactions within the same area remain insufficiently understood, leaving the drivers of niche differentiation between the two species unclear.

To provide insights into the environmental variables underlying niche differentiation of the two *Ammodytes* species, we developed a species distribution model based on buried sandeel collected during the Dutch annual coastal shellfish survey. Our aim was to describe the buried distribution of *A. tobianus* and *A. marinus* along the Dutch coast and investigate potential differences between the two species. The model included environmental variables such as sediment characteristics (median grain size and silt fraction), salinity, and depth. Given that sandeel prefer penetrable sediments for burrowing and are known to avoid substrates with high gravel content, we additionally investigated the effect of local bivalve biomass on sandeel presence, as high densities of bivalves may alter sediment structure and reduce its suitability for burrowing. Finally, we examined species-specific temporal aspects of sandeel behaviour by including day-of-year and relative time-of-day variables. This study provides new insights into niche differentiation between sandeel species in both spatial distributions and behaviour within the same geographical area. More broadly, it contributes to our understanding of potential species-specific differences in their role as key prey in coastal ecosystems.

2. METHODS

2.1. Sampling

Buried sandeel were collected, as bycatch, in the annual Dutch coastal shellfish survey, which is designed to monitor stock sizes of commercially interesting shellfish species in an area up to approximately 12 nautical miles offshore (Troost et al., 2024). This survey is conducted by Wageningen Marine Research and commissioned by the Dutch government ('Wettelijke Onderzoekstaken',

WOT), hereafter referred to as the WOT survey. Although the WOT survey employs several types of sampling gear (Troost et al., 2024), we exclusively used sandeel data obtained with a towed bottom cutting dredge. This dredge is equipped with a 9-10 cm wide cutting blade that penetrates 10 cm into the sediment, enabling the capture of sandeel typically buried at depths of 1–4 cm (Behrens et al., 2007). However, during sampling, approximately 50% of captured sandeel were damaged (including individuals cut in half), likely due to last-moment escape attempts by moving sideways or burrowing deeper into the sediment. Including the half-cut individuals reduces the risk of under-sampling individuals along the edges of the bottom cutting dredge. On board, the catches are sieved over a 5 mm mesh (Troost et al., 2021). Haul lengths, measured either with a measuring wheel or derived from GPS positions, are typically about 150 m, except in the southern delta area (Voordelta) where they are approximately 75 m, corresponding to sampled surface areas of ~15 m² and ~7.5 m², respectively (Troost et al., 2021). We analysed sandeel data collected over two periods: 2016-2018 and 2020-2022. A total of 4,073 locations were sampled during daytime, mostly between 08:00 and 20:00, from March to June (Fig. S1). The spatial order in which locations were sampled varied among years (Fig. S2). Due to COVID-19 restrictions in 2020, sampling was conducted only between 25 May and 9 June (Troost et al., 2024). Moreover, sandeel were not collected in the last 2 weeks in 2020, therefore, the sampling points in those weeks were excluded from the analysis to avoid false zeros. All sandeel were frozen on board for subsequent laboratory analysis. In the laboratory, individuals were identified to species level, length measured to the nearest 0.1 cm, and mass recorded to the nearest 0.01 g (scale: Mettler Toledo ICS429). At stations with large catches, a subsample of sandeel was individually measured and weighted, while the remaining intact individuals were weighed together, and all damaged individuals were also weighed collectively.

2.2. Species identification

Sandeel species captured during the shellfish survey include *A. marinus, A. tobianus* and *H. lanceolatus.* Species identification was based on morphological characteristics (Macer, 1966; Reay, 1970; Thiel & Knebelsberger, 2016) and included the diagnostic feature of the M-band at the base of the caudal fin (van Deurs et al., 2012). First, the *Ammodytes* species were separated from *H. lanceolatus*, by examining the protrusible premaxilla, vomerine teeth, a black spot on the snout, and the general shape of the head. Subsequently, the two *Ammodytes* species were distinguished by the absence of scales over the musculature at the base of the caudal fin (*A. marinus*) versus the presence of an M-band pigmentation line (*A. tobianus*). From a subset of individuals, a small muscle tissue sample was taken for DNA-based identification. Sanger sequencing of the

mitochondrial COI and nuclear rhodopsin gene (Thiel & Knebelsberger, 2016) and rapid screening via qPCR methods (see Chapter 4) was applied to identify juveniles and/or damaged specimens, particularly from locations with few intact sandeel. In addition, DNA analyses were used to validate the accuracy of identifications based on the morphological traits described above. Individuals, without a selection based on size or damage, showed that 92% of *A. marinus* and 77% of *A. tobianus* were correctly identified.

2.3. Data processing

In the first sampling period (2016–2018), species identification was based solely on morphological analysis of intact individuals. For fish collected in the second period (2020–2022), we also attempted to identify damaged individuals with only either a head or a tail. Because head and tail counts often differed at a single sampling location, the total count for each species was taken as the maximum of either heads or tails. When the number of heads exceeded the number of species identified on the tails, the remaining heads were classified as *Ammodytes* spp. At sampling locations where the number of *Ammodytes* spp. was ≥4 and at least four individuals were identified to species level, the ratio of the identified species was used to assign species identity to the remaining *Ammodytes* spp.

2.4. Environmental variables

Depth data (resolution ~115 m) were obtained from the European Marine Observation and Data Network Bathymetry Consortium Portal (EMODnet). Sediment median grain size (D50) and mud (<63 µm) percentage (resolution 200 m) were sourced from the TNO Geological Survey of the Netherlands via Deltares OPeNDAP (downloaded in June 2025; now available only upon request). Average bottom salinity for the period 2003–2017 (resolution ~5 km) was derived from the northwest European shelf implementation (van der Molen et al., 2016; van der Molen et al., 2021) of the General Estuarine Transport Model (GETM; Burchard & Bolding, 2002). These environmental variables were assigned to the sandeel sampling points by using the nearest neighbour distance (Fig. S3). Five bivalve metrics (Fig. S4) were derived from the Dutch coastal shellfish survey and accessed via Rijkswaterstaat Informatiehuis Marien (https://ihm.nl/open-data-viewer/). These metrics, expressed in g m^{-2}, included: (1) wet weight of *Spisula subtruncata*, (2) wet weight of *Ensis directus*, (3) combined wet weight of *S. subtruncata* and *E. directus*, (4) total wet weight of all bivalve species recorded in the WOT survey (referred to as "bivalves" despite including a few non-bivalve species; see Table S1 for the full species list), and (5) total wet weight of all shellfish species excluding *S. subtruncata* and *E. directus*. The latter metric was included to assess the effect of shellfish species that contribute

only relatively little to the total biomass in the study area. In addition, the total catch volume of the dredge sample was used as a sixth metric to capture the abundance of both living and dead bivalves, though this also includes other benthic taxa such as crabs and sea urchins. These bivalve metrics were directly linked to the sandeel observations, as they originated from the same haul. We did not test additional environmental variables, as many are (indirectly) linked and thus correlated to sediment characteristics (e.g., current speed) or depth (e.g., temperature, light). We limited the models to one sediment variable (either median grain size or mud content) and one bivalve metric (the best-performing one). All environmental variables included in the final models were checked for collinearity, and no issues were detected.

2.5. Model structure

To identify species-specific seabed habitat preferences, dependencies on temporally dynamic variables, and the geographical distributions of *A. tobianus* and *A. marinus*, we fitted models using the Integrated Nested Laplace Approximation (R-INLA) framework (Lindgren & Rue, 2015). The Stochastic Partial Differential Equation (SPDE) approach (Lindgren et al., 2011) was used to estimate residual spatial heterogeneity as latent fields, which represents spatial variation not explained by other covariates. The SPDE approach requires a mesh to capture spatially structured random components and generate the latent fields. The mesh consisted of triangles with a maximum edge length of 6.7 km and a cutoff distance of 1.3 km, resulting in 3,131 nodes (Fig. S5).

Abundances of each species were modelled using a Negative Binomial distribution with mean μ, dispersion parameter k, and a log link function which were defined as follows (Devroye, 1986):

$$y_{sj} \sim NB\left(\mu_{sj}, k\right) \tag{1}$$

$$E\left(y_{sj}\right) = \mu_{sj} \tag{2}$$

$$var\left(y_{sj}\right) = \mu_{sj} + \frac{\mu_{sj}^2}{k} \tag{3}$$

$$log\left(\mu_{sj}\right) = SpeciesYear_s + f\left(relative\ time - of - day_{sj}\right) + f\left(DOY_{sj}\right) + f\left(environmental\ covariates_{sj}\right) + offset\left(log\left(sampling\ area_{sj}\right)\right) + v_{sj} \tag{4}$$

where y_{sj} represents the observed count of the species *s* in sample *j*. The expected mean μ_{sj} was modelled as a function of species-specific year intercepts, species-specific explanatory variables, a sampling surface offset (log-transformed to account for the exponential link), and species-specific spatial fields v_{sj} (Schultz et al., 2025). The species-specific year intercepts allowed each species to have its own baseline abundance for each year. A "relative time-of-day" variable was included in the models to account for the daily vertical migration of sandeel, as their presence in the water column (and thus their presence in the seafloor sediment) varies throughout the day in the foraging period (Baker et al., 2023; Freeman et al., 2004; Komiyama et al., 2024). This variable was scaled so that 0 corresponds to sunrise and 1 to sunset, thereby adjusting for changing day length across the sampling period. Because water column presence is also not constant throughout the foraging season (Henriksen et al., 2021), a day-of-year (DOY) component was also added to the model to account for seasonal variation. The environmental variables were added to identify spatial patterns and seabed habitat preferences. All explanatory covariates were specified as species-specific predictors, allowing the effect of each variable to differ between *A. marinus* and *A. tobianus*. Non-linear relationships with the response variables were accounted for by using four-degree polynomial functions (Schultz et al., 2025). Automatic selection of the number and placement of knots was not readily available within the statistical modelling framework we used in this study (but see Anderson et al., 2025). The natural logarithm of the sampled surface area was added as an offset to account for variation in sampling effort without introducing additional parameters. The species-specific latent fields (v_{sj}), share hyperparameters for spatial range and marginal variance across both species. The latent fields, year effect, temporal components, and the sampled surface area offset were included in all tested models and are therefore referred to as the "base" part (see Table 1).

To identify the best-fitting model, environmental variables were selected based on the Watanabe-Akaike Information Criterion (WAIC). Only the best bivalves metric, based on the WAIC value, was used to combine with the other environmental variables. Model validation was then performed separately for *A. marinus* and *A. tobianus*, following the procedures described by Zuur et al. (2017). Pearson residuals were calculated for each observation and examined against fitted values and individual covariates. Spatial structure in the residuals was assessed using sample variograms. Model predictions were compared with observed counts by inspecting the resulting histograms (Fig. S6). Finally, the model's ability to account for the high number of zeros was evaluated by comparing the observed number of zeros with the number predicted across posterior samples (Fig. S6).

2.6. Spatial prediction

A spatial grid with 1 × 1 km cells was created to predict the abundance of *A. marinus* and *A. tobianus* in the Dutch coastal zone. Environmental covariates were assigned to each grid cell using the nearest neighbour values. Bivalve biomass used for the prediction was calculated by creating a 5 km radius buffer around each grid cell and assigning to each cell the mean biomass of all samples from all sampling years within that buffer. This approach produced a generalized bivalve layer for prediction (Fig. S7) rather than a year-specific pattern. Consequently, predictions were limited to areas within ~5 km of the sampling locations, as the bivalve layer contains no data beyond this range. To avoid making predictions beyond the range of observed environmental conditions, values of each environmental variable in the prediction grid were constrained to the minimum and maximum value observed at the sandeel sampling locations (Fig. S8). Any value outside this range was replaced with the corresponding observed limit. For the prediction, relative time-of-day was set to 0.5, day of year (DOY) to 150 (end of May), and 2022 included as the species-specific year effect. As sampling was conducted only during daylight hours and not at night—when all sandeel are buried in the seabed—the predicted values represent relative densities. The chosen time-of-day and DOY serve as scaling references and do not influence spatial patterns. Therefore, these values were selected to roughly correspond to the midpoint of the sampling periods. The year 2022 was selected as the most recent sampling year with relatively moderate sandeel mean abundance (Fig. S9). Lastly, the species-specific latent fields, estimated on the irregular SPDE mesh, were interpolated onto the regular 1 × 1 km grid and included in the predictions.

3. RESULTS

3.1. Survey data

In total, 5,860 *A. marinus*, 1,685 *A. tobianus*, and 1,040 (unidentified) *Ammodytes* spp. were recorded. These individuals were distributed across 1,432 stations (35% of all sampling locations), with 33 stations (0.8%) containing more than 50 individuals (Fig. 1). The mean sandeel density was 0.046 individuals per m², with *A. marinus* occurring at a higher mean density (0.09 individuals per m²) than *A. tobianus* (0.03 individuals per m²). Densities also varied between years, with relatively high values observed in 2020 (when fewer offshore stations were sampled) and 2022 (Fig. S9). Furthermore, lengths of the (undamaged) sandeel were similar, with *A. marinus* ranging from 4.3 to 17.8 cm (mean 10.5 cm) and *A. tobianus* ranging from 4.4 to 18.6 cm (mean 10.4 cm). However, the length distribution of A. tobianus generally showed a wider spread within years com-

pared to *A. marinus* (Fig. 2). This was particularly evident in 2022, when a narrow and small-sized cohort of *A. marinus* was observed, in contrast to the broader size range of *A. tobianus* in the same year. Furthermore, between-year temporal variability is apparent for *A. marinus*: in 2016 and 2017, relatively large individuals (many ≥15 cm) were caught along with few small ones, whereas in later years, catches were dominated by smaller individuals (<10 cm) and included fewer large ones. No such clear temporal variability was apparent for *A. tobianus*.

3.2. Observed catch distribution

Figure 1 shows that *A. tobianus* was primarily found in coastal areas shallower than 20 m, hereafter referred to as nearshore areas, particularly around the Wadden Sea inlets, along the northern west coast (North Holland province), and in the southern delta region (Voordelta). In contrast, areas deeper than 20 m, hereafter referred to as offshore areas, including those north of the Wadden Islands and off the northern west coast, were dominated by *A. marinus*. Despite these general patterns, both species were also found to overlap in several areas within the same sampling year, especially near the Wadden Islands and in the offshore Voordelta area. Not only did their distributions overlap geographically, but both species were also captured in the same sampling hauls, highlighting fine-scale co-occurrence (Fig. S10). Conversely, both species were less frequently caught along the southern part of the west coast (South Holland province), and north of Ameland. Distribution and abundance patterns also varied between years. In 2020, *A. marinus* occurred at particularly high densities offshore north of the Wadden Islands, whereas in 2022, its highest densities were observed closer to the Wadden Islands. In comparison, spatial patterns for *A. tobianus* were more stable, although in 2021 *A. tobianus* was more abundant and distributed over a wider geographical area.

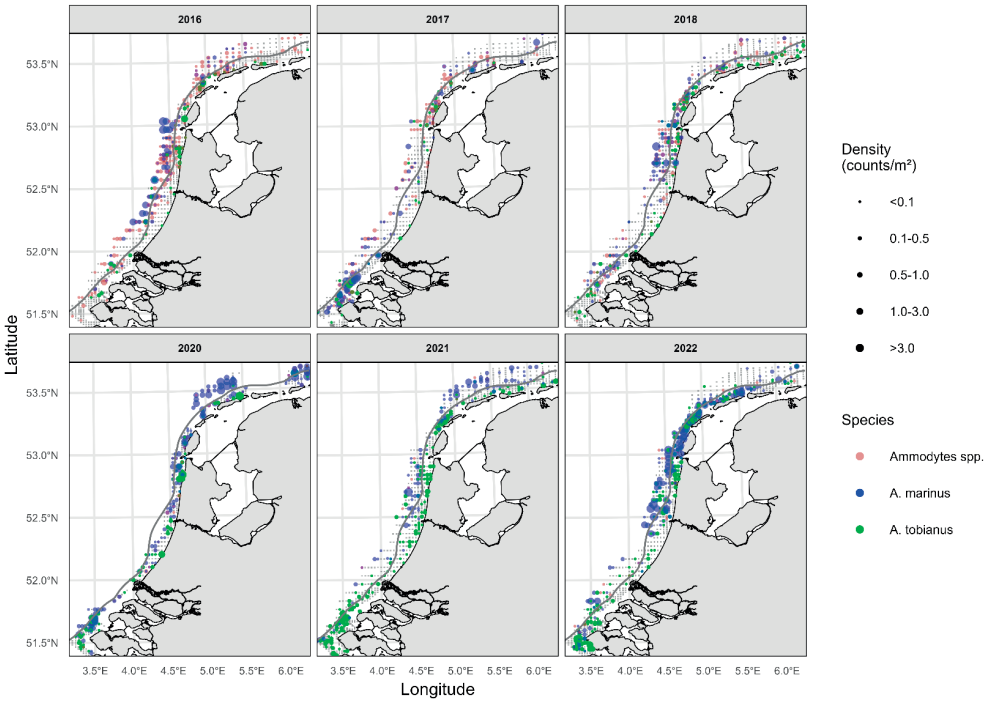


Figure 1: Observed densities of A. marinus (blue circles), A. tobianus (green circles), and unidentified *Ammodytes* (red circles) per year. Small grey dots indicate sampling locations where no sandeels were caught. The smoothed 20 m depth contour is shown in grey.

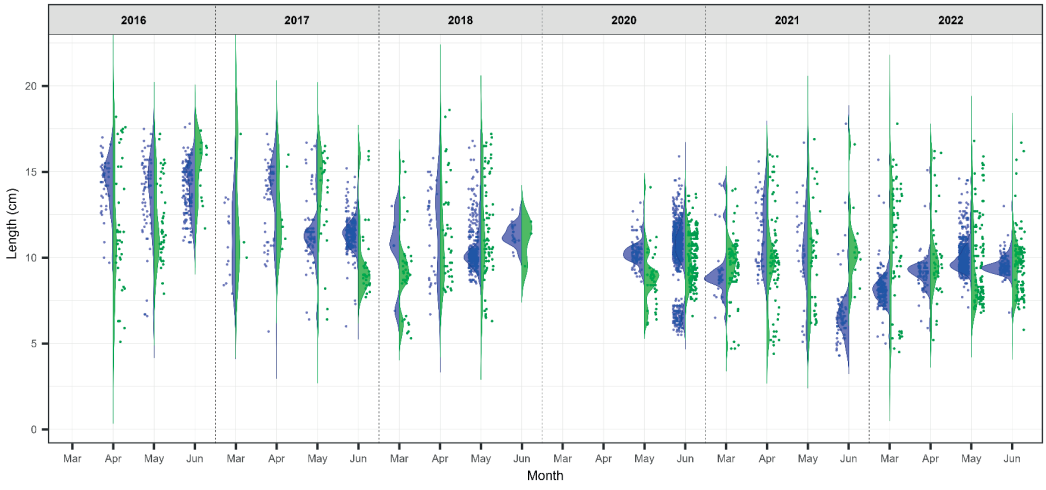


Figure 2: Observed sandeel lengths by species (blue = A. marinus, green = A. tobianus), year, and month. Violin plots show the distribution of lengths (cm) for each species, with points representing individual observations. Only intact individuals are included.

3.3. Effects of explanatory variables

We tested a range of variables to understand the drivers of sandeel distribution and species-specific differences. Adding median grain size, mud or salinity only marginally improved the base model (Table 1). In contrast, models that included depth or bivalves metrics showed substantial improvements in model fit, with all bivalve biomass (hereafter "total bivalve biomass") providing the best model performance among the six metrics tested. For models with two environmental variables, the combination of total bivalve biomass and depth produced the best fit, which was further slightly improved by adding salinity, although this improvement is not visible in Table 1 due to rounding. All subsequent results are therefore based on this best-fitting model, which included depth, total bivalve biomass, and salinity as spatial predictors. The effective number of parameters generally decreases in better-fitting models, most likely because less complex and heterogenous latent fields were needed to capture the spatial distribution of sandeel density.

Table 1. Overview of model outcomes, ordered by decreasing WAIC values, capturing the spatial patterns of both *Ammodytes* species. The 'Base' model includes species-specific year intercepts, a species-specific latent field (unexplained variance), relative time-of-day, and day of year (DOY) variables. All shellfish metrics are shaded in grey. The best model, based on the lowest WAIC value, is indicated in bold. This model is also taken as reference for ΔWAIC.

Model	Eff. Parameters	WAIC	ΔWAIC
0 environmental variables			
Base	460	15576	244
1 Environmental variable			
Base + Median grain size	467	15575	243
Base + Mud content	470	15575	243
Base + Salinity	473	15571	239
Base + Depth	430	15517	185
Base + Bivalve (bivalves species excluding Ensis and Spisula)	425	15480	148
Base + Bivalve (Spisula)	444	15478	146
Base + Bivalve (Ensis)	447	15469	137
Base + Bivalve (Catch volume)	438	15459	127
Base + Bivalve (Spisula + Ensis)	433	15413	81
Base + Bivalve (All bivalve species)	426	15383	51
2 Environmental variables			
Base + Bivalve (All bivalve species) + Mud content	434	15388	56
Base + Bivalve (All bivalve species) + Median grain size	431	15386	54
Base + Bivalve (All bivalve species) + Salinity	440	15379	47
Base + Bivalve (All bivalve species) + Depth	394	15332	0
3 Environmental variables			
Base + Bivalve (All bivalve species) + Depth + Median grain size	403	15336	4
Base + Bivalve (All bivalve species) + Depth + Mud content	404	15336	4
Base + Bivalve (All bivalve species) + Depth + Salinity	**404**	**15332**	**0**
4 Environmental variables			
Base + Bivalve (All bivalve species) + Depth + Salinity + Median grain size	412	15335	3
Base + Bivalve (All bivalve species) + Depth + Salinity + Mud content	413	15335	3

3.4. Temporal and spatial relationships

The model outcomes revealed clear temporal and spatial patterns in sandeel density (Fig. 3). Throughout the day, density increased from afternoon to evening, with a slightly stronger effect observed for *A. marinus* (Fig. 3a). The overlapping credible intervals indicate that, apart from the evening, differences between species were not substantial. In contrast, clear differences were found in seasonal trends. *A. marinus* densities were lowest in early April (DOY 90–100) and peaked in late June (DOY >175). *A. tobianus*, on the other hand, showed a parabolic pattern, with lowest densities in late April to early May (DOY ~120) and higher densities at both the beginning and end of the season (Fig. 3b), the latter slightly exceeding densities observed at the start of the season. Spatially, depth effects were also species-specific: *A. tobianus* densities decreased at depths exceeding 15 m, whereas *A. marinus* showed no clear depth preference (Fig. 3c). Both species were strongly negatively associated with total bivalve biomass (Fig. 3d). Salinity also influenced counts, though its effect was relatively weak, with credible intervals largely overlapping zero (Fig. 3e). Nevertheless, *A. tobianus* appeared to prefer slightly lower salinities (~29 PSU) compared to *A. marinus* (~32.5 PSU).

These environmental variables did not capture all species-specific spatial patterns observed as indicated in Figure 4. For *A. marinus*, areas where densities were higher than predicted by the included covariates, shown in red, were mainly located offshore along the west coast and in waters northwest of the Wadden Islands. Conversely, areas where densities were lower than predicted, shown in blue, occurred in the nearshore zone of the west coast, inshore parts of the southern delta, and waters north of Ameland and Schiermonnikoog. For *A. tobianus*, areas with higher-than-predicted counts were mainly distributed along the entire west coast and west of the Wadden Islands, while lower-than-predicted counts were in the inshore Voordelta and offshore waters north of Terschelling and Ameland.

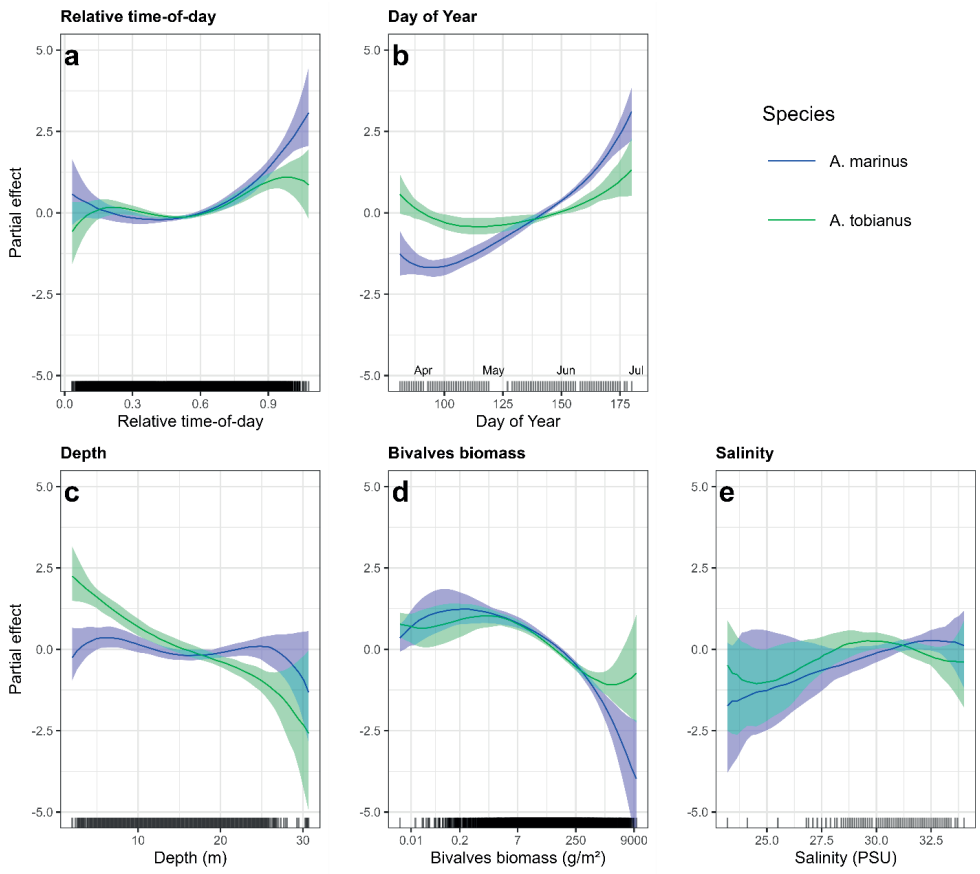


Figure 3: Partial effects of (a) relative time-of-day, (b) day of year (DOY), (c) depth, (d) bivalve biomass, and (e) salinity on the densities (log scale) of two *Ammodytes* species. Shaded areas represent 95% credible intervals. For relative time-of-day, 0 corresponds to sunrise and 1 to sunset. Month labels on the DOY axis indicate the first day of each month. Tick marks on the x-axis represent observed data points

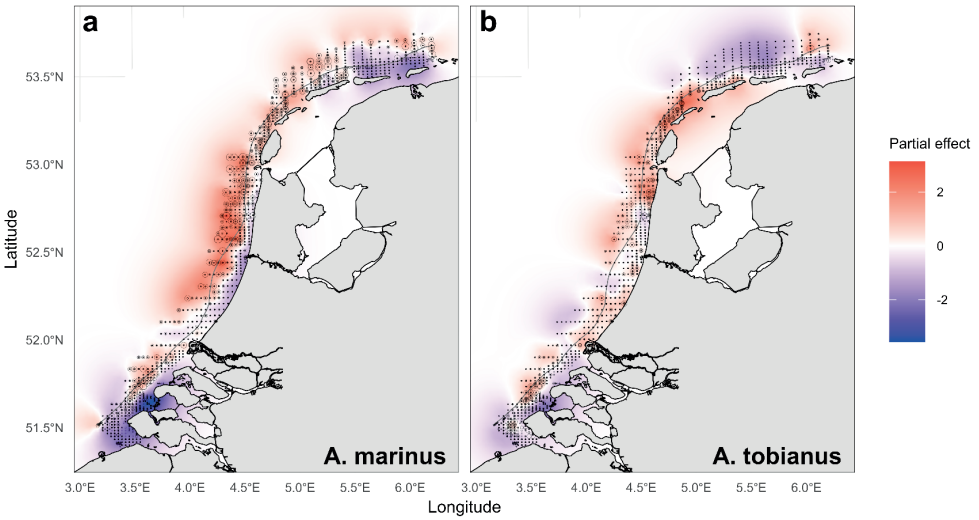


Figure 4: Posterior mean of the latent field for the densities (log scale) of (a) A. marinus and (b) A. tobianus. The latent field represents spatial variance (log scale) not explained by the other model variables. Red areas indicate regions where counts were higher than predicted by the other variables, while blue areas indicate regions where counts were lower. Circle size corresponds to observed sandeel counts, with a dot indicating zero catch. The smoothed 20 m depth contour is shown in grey.

3.5. Predicted distribution

The predicted spatial distributions of both *Ammodytes* species reveal a general nearshore–offshore separation (Fig. 5). However, the distributions of the two species also overlapped, particularly near the Wadden Islands and along the 20 m depth contour in the southern delta region. The density estimates are conservative, as the midday predictions (see Fig. S11 for sunset predictions) at the end of May do not represent maximum abundances. Furthermore, only specimens identified to species level are included in the species-specific predictions. The estimates show that the highest predicted densities of *A. marinus* (up to 2 individuals per m^2) were found relatively offshore along the west coast, whereas *A. tobianus* reached its highest densities (up to 0.7 individuals per m^2) near the southwestern Wadden Sea tidal inlets and a specific location in the southern offshore delta. The avoidance of areas with high bivalve biomass (Fig. S7) is clearly reflected in the low densities of *A. marinus* north of Ameland, as well as in a distinct low-abundance area around 52.5°N. Spatial uncertainty in the model prediction is highest towards the edges and in deeper areas of the study area (Fig. S12). Year-specific maps of spatial Pearson residuals (Fig. S13) show the year-to-year spatial variations in distribution that are not accounted for in the model.

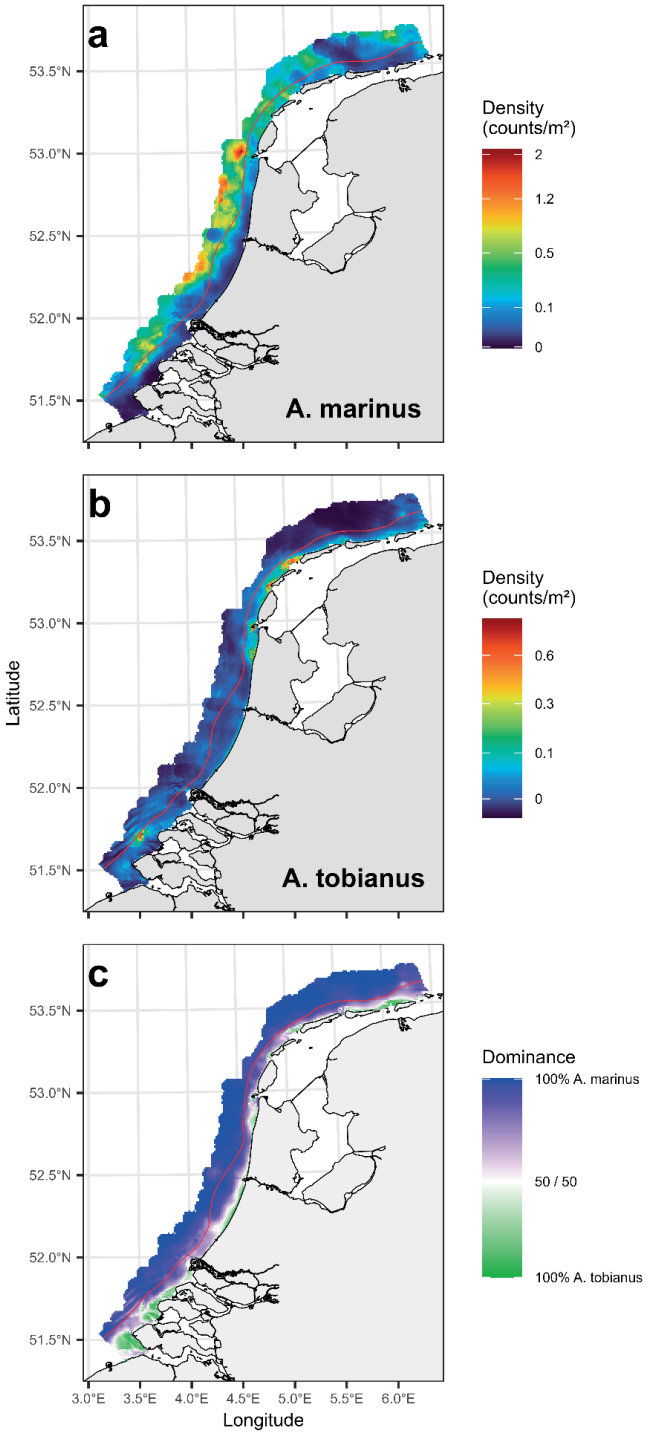


Figure 5: Predicted distribution (in counts per m^2) of (a) A. marinus, (b) A. tobianus, and (c) their relative dominance, along the Dutch coast. The smoothed 20 m depth contour is shown in red. Note the different scale ranges used for the two species.

4. DISCUSSION

In this study, we found that the two *Ammodytes* species generally differ in their spatial distributions, with *A. marinus* occurring at higher abundances in offshore waters and *A. tobianus* more commonly occurring in nearshore habitats. Depth, and to a lesser extent salinity, were identified as the main drivers of niche differentiation. However, substantial spatial variation remained unexplained, indicating that key factors driving their niche and thus niche differentiation are still unidentified. However, some areas of spatial overlap were observed, with both species displaying similar pronounced avoidance of high bivalve biomass. This geographical overlap indicates that they do not exhibit strict spatial segregation, and also no behavioural differences in daily seabed presence were identified that could explain niche differentiation.

4.1. Spatial patterns

The observed overlapping distribution (Fig. 5) of both species in the Wadden Sea tidal inlets and the southern delta region are consistent with previous observations (Tien et al., 2017; van Hal et al., 2021). They also align with the winter distribution of unidentified sandeel in the Dutch Exclusive Economic Zone, which was based on data collected over a coarser, less coastal-oriented grid and with a different demersal sampling gear (Chapter 2). In this study, we found that the observed distributions were best explained by depth, total bivalve biomass and salinity. Depth, which is highly collinear with several other environmental variables such as temperature, salinity, primary and secondary productivity, and sediment type (Costello et al., 2018), partially captured the offshore–nearshore segregation of each species.

The density of both *Ammodytes* species was strongly negatively associated with bivalve biomass. One hypothesis is that high shell content in the sediment may act as a physical barrier to burrowing. While previous studies have not directly examined the effect of shell content on sandeel burying behaviour, Henriksen et al. (2024) reported based on experimental trials that *A. tobianus* avoided sediments containing 30% gravel (4–8 mm), which was also attributed to the gravel acting as a barrier to burrowing. Similarly, field observations in the Dutch part of the North Sea indicated that gravel areas were also less preferred by sandeel (Witbaard et al., 2024). Another hypothesis is that the (in-situ) measurements of bivalve biomass may act as a proxy for other (abiotic) environmental variables, like sediment type, which in this study has been derived from more broad-scale sediment maps. For example, *Spisula subtruncata*, a major contributor to total shell biomass (see Table S1), reaches its highest densities in medium-fine sediments within our study area (160–280 µm; de Fouw et al., 2024). *Ensis directus*,

another important contributor to total shell biomass, is most abundant in the muddiest sediments along the Dutch coast, also because their presence results in siltier sediment (Witbaard et al., 2017). Thus, a negative relationship between bivalves and sandeel abundance may reflect not only barriers from high shell content, but also represents sediment types that are less suitable for sandeel, for example, the silty sediments preferred by *E. directus*. Catch volume, which also included dead shells, might provide a more direct measure of potential barriers for burrowing. However, this metric performed worse than total bivalve biomass to explain sandeel abundance. A possible explanation is that catch volume also contained other benthic groups (e.g., crabs, sea urchins) that may not act as strong burrowing barriers. Experimental studies that manipulate shell content and shell types, including different species and distinguishing between living and dead shells, could provide more detailed and direct insights into this potential barrier effect.

Salinity was expected to explain a larger proportion of the spatial separation between the species than the relatively small effect found in this study, as *A. tobianus* is more coastal and can occur in brackish waters, unlike *A. marinus* (Henriksen et al. 2024). However, the 95% credible intervals for both species largely overlapped across the salinity gradient, indicating that differences were not substantial (Fig. 3e). This may be because we used long-term averages, whereas other aspects of salinity—such as short-term fluctuations, extremes, or season-specific conditions—are potentially more important drivers of species distribution.

The latent fields (Fig. 4) revealed substantial unexplained spatial variation, indicating that depth, benthos, and average salinity alone could not fully explain the observed spatial distributions. Sediment characteristics (grain size and mud content) were expected to play a strong role, as numerous studies (Holland et al., 2005; Langton et al., 2021; Tien et al., 2017; Wright et al., 2000) link sandeel distributions to coarse, sandy substrates with low mud content. As shown in Fig. S14, *A. marinus* avoided fine sediments and both species displayed a slight preference for low mud values, however, a strong sediment effect could not be detected. This may be due to (1) the relatively limited variation in sediment grain size in our study area and (2) the use of a relatively outdated sediment data map. The latter may poorly reflect the exact sedimentary conditions at the sampling stations, especially given the high dynamics in the study area, characterized by e.g. moving sand dunes (Cheng et al., 2020).

A factor that the latent field seems to capture is the spillover of *A. tobianus* from the Wadden Sea, where *A. tobianus* is dominant over *A. marinus* with a

4:1 ratio (Maathuis et al., 2025a), into the North Sea side of the tidal inlets. At these inlets, both species occur in roughly equal numbers (Fig. 5). It suggests that the Wadden Sea is presumably the preferred habitat of *A. tobianus*, with the immediate adjacent areas in the North Sea still falling within its suitable habitat range. Another aspect that may be partially captured in the latent fields is the effect of larval dispersal, an important driver of sandeel distributions (Christensen et al., 2008). At the North Sea scale, *A. marinus* populations along the Dutch coast receive little influx from other regions (Christensen et al., 2008), but at a local scale, larval transport likely influences the distribution of both species. For instance, large numbers of post-larval *Ammodytes* spp. were observed in Isaacs–Kidd net samples from the western Wadden Sea in 2010 and 2012 (WMR, unpubl. data). However, (post)larval dispersal has not been studied in more detail for this area, particularly not at the species level, making it difficult to explicitly account for in the spatial models. Finally, predation pressure may also contribute to the unexplained spatial structure captured by the latent fields. Predators such as seals, porpoises or seabirds may influence spatial patterns, particularly because predation by central place foragers (such as seals and many chick-feeding seabird species) is higher near colonies or resting sites than in more distant areas (Aarts et al., 2019; Furness, 1990), which can lead to local depletion known as Ashmole's halo (Birt et al., 1987).

4.2. Temporal patterns

The model's temporal variables offered potential insights into the behaviour of sandeel. The Day of Year (DOY) explanatory variable (Fig. 3) revealed a clear seasonal trend: an increasing density of sandeel in the sediment from mid-April onwards for *A. marinus* and from May onwards for *A. tobianus*, with the seasonal rate of increase being more pronounced for *A. marinus*. A similar pattern has been observed acoustically in the Norwegian part of the North Sea, where fewer *A. marinus* were found in the water column in June compared to May, likely reflecting more individuals remaining in the sediment (Komiyama et al., 2024). Closer to our study area, Henriksen et al. (2021) examined seasonal emergence of *A. marinus* into the water column using commercial catches from the central and eastern North Sea. They found that most sandeel were active in the water column from late April until mid-May (DOY 110–135), depending on location and year, which aligns with our observation of the lowest occurrence in the sediment for that same period.

The relationship with time-of-day revealed that sandeel were least abundant in the seabed around noon and gradually return to the seabed towards sunset. This pattern is consistent, though reversed because we sampled sandeel buried in the seabed, with acoustic observations of sandeel in the water

column (Komiyama et al., 2024). Komiyama et al. (2024) found that sandeel schools were more abundant in the water column during the morning than in the afternoon. This pattern may reflect morning foraging followed by a return to the sediment once satiated. Similarly, other studies have reported lower water column presence in the late afternoon compared to the morning (Baker et al., 2023; Freeman et al., 2004). However, instead of high presence throughout the day, these studies observed that presence of sandeel in the water column was primarily concentrated at dawn and dusk.

Baker et al. (2023) furthermore suggested that offshore–nearshore location and sandeel size may influence diurnal behaviour. Komiyama et al. (2024) also observed a seasonal effect in diurnal behaviour, with lower presence in the water column during dusk in June than in May. They attributed this to a decline in foraging motivation towards the end of the foraging season. We did not assess whether seasonal, spatial, or size-related factors contributed to the observed time-of-day pattern. We did, however, observe that presence in the seabed was lower in the morning than in the evening, suggesting that sandeel became active before sunrise. Baker et al. (2023) observed *A. personatus* entering the water column 30–45 minutes before sunrise in experimental tanks. However, our study could not confirm the exact timing, as sampling took place only during daylight hours. Nor could we verify whether presence in the seabed at sunset represented a maximum or if sandeel continued returning to the seabed afterwards.

The observed diurnal pattern in sandeel behaviour also appears to be reflected in prey selection of sandwich terns, which fed fewer sandeel to chicks toward evening and increasingly switched to herring as an alternative food source (Stienen et al., 2000). Comparable predator responses have been documented in humpback whales, which conducted more surface feeding during the day and more bottom feeding at night (Friedlaender et al., 2009), and in whiting and haddock, where sandeel occurrence in stomachs peaked at night in summer (Temming et al., 2004). Likewise, sandeel availability shapes predator foraging behaviour also on a seasonal scale, with changing proportions in predator diets throughout the year (Greenstreet et al., 1998; Wanless et al., 1999; Wilson & Hammond, 2019).

Yearly abundance trends are also reflected in sandeel predators. For instance, seabird breeding success is strongly linked to sandeel abundance (Rindorf et al. 2000, Régnier et al. 2024). We did not observe that either 2017 or 2018 was a particularly good sandeel year with high overall density (Figs. S9 and S15). This contrasts with the December dredge data from the ICES North Sea Sandeel

Survey (NSSS), which reported relatively high densities of sandeel in 2017 at three locations in the Dutch coastal zone (Fig. S16). This difference may suggest that yearly trends within the Dutch coastal zone may vary spatially. For example, the NSSS coastal sampling locations are all near Texel, whereas our dataset covers the entire Dutch coast. Future work could investigate these spatial differences in yearly trends in more detail. Alternatively, the observed discrepancies may also reflect differences in the timing of the surveys (December versus spring).

The observed seasonal and inter-annual trends might also be partly confounded by time-varying catchability effects, as sandeel grow throughout the sampling season from March to June and smaller individuals are probably less likely to be retained by the sampling gear. For example, in 2020 and 2021 two cohorts of small *A. marinus* individuals (mean size ~6–7 cm) were caught late in the season (June; Fig. 2). These cohorts might have been undetected earlier in the season because they were too small for the sampling gear. Similar pronounced small *A. tobianus* cohorts were not caught late in the sampling season, which may reflect differences in spawning periods between the species (Bergstad et al., 2001; Reay, 1970). Other factors affecting catchability, such as changes in water temperature, tides, or turbidity, may also have contributed. Consequently, observed patterns in sandeel presence in the seabed likely reflect a combination of behavioural changes and catchability effects.

4.3. Species overlap and niche differentiation

Habitat, time, and diet are generally recognised as the main aspects, or dimensions, of niche differentiation (Schoener, 1974; Sawada et al., 2025). Our study shows that the two *Ammodytes* species are generally segregated but can locally coexist along the Dutch coast, even within the same haul. This was particularly evident in 2022. The overlap suggests that their seabed habitat preferences and tolerances are very similar and that habitat alone does not fully explain niche differentiation. In addition to seabed habitat, differences in foraging habitat and prey selection may play an important role in niche differentiation. For example, *A. marinus* and *A. tobianus* may move to different areas to feed or may feed in different vertical layers of the water column and/or feed on different prey types. Future studies could explore this further, for example using (PIT) tagging.

For the second niche dimension, time (or timing), daily vertical migration in and out of the sediment did not differ between the two sandeel species. For instance, no evidence was found that one species predominantly occupies the water column in the morning while the other does so in the afternoon, indicating an absence of temporal niche differentiation. It should be noted, however, that

the observed temporal patterns are based on data from the entire study area and may differ in locations where the two species co-occur.

The third dimension of niche differentiation, diet, remains poorly understood for the two species in our study area, as no species-specific dietary studies have been conducted. However, interannual abundance patterns indicate that high-abundance years for one species did not necessarily correspond to low-abundance years for the other. This may suggest that food competition between the species is not a primary driving factor, either because they require different foraging conditions (e.g., turbidity plays a role), or because they utilize different food resources. As sandeel diet is largely constrained by mouth size, which scales with body length (O'Connell & Fives, 1995), length likely plays an important role. Indeed, the peaks in the length distributions of the two species differ (Fig. 2), which may suggest potential dietary differences. Therefore, incorporating a length component into statistical models could provide further insight into sandeel niche differentiation.

4.4. Practical implications

This study demonstrates that benthic sampling, alongside acoustic and experimental approaches, can provide valuable insights into behavioural patterns of sandeel. In addition, we found that, beyond sediment grain size characteristics, seabed factors such as the presence of living and dead shells may play an important role in sandeel habitat preferences. Finally, the resulting distribution maps, as well as the interannual, seasonal and daily trends, yield insights that can also help in our understanding of sandeel–predator interactions and, consequently, the pivotal role of sandeel, also at the species level, as key forage fish.

Acknowledgements

This work was funded by the Netherlands Organization for Scientific Research (NWO) through Top Sector Water & Maritime under the project name "Forage Fish" (NWO- TWM.81.019.008), co-funded by the Dutch Ministry of Infrastructure and Water Management (RWS). Also, the Ministry of Agriculture, Fisheries, Food security, and Nature (LVVN) financially supported this project. The contribution of Geert Aarts and Sophie Brasseur to this manuscript, was funded through HORIZON EUROPE program ACTNOW: Advancing understanding of Cumulative Impacts on European marine biodiversity, ecosystem functions and services for human wellbeing (Grant no. 101060072). We thank the crew of the *Isis* from Rijkswaterstaat, as well as Wageningen Marine Research colleagues: Karin Troost, project leader of the benthic shellfish surveys; Johan Cruijmeersch, for his feedback on the manuscript; and Margriet van Asch, for

her assistance and advice on data-related questions. We also want to thank Jan Jaap Poos for his input in the INLA analysis.

DATA AVAILABILITY

Data and R-code is available at https://doi.org/10.25850/nioz/7b.b.1k

SUPPLEMENTARY MATERIAL

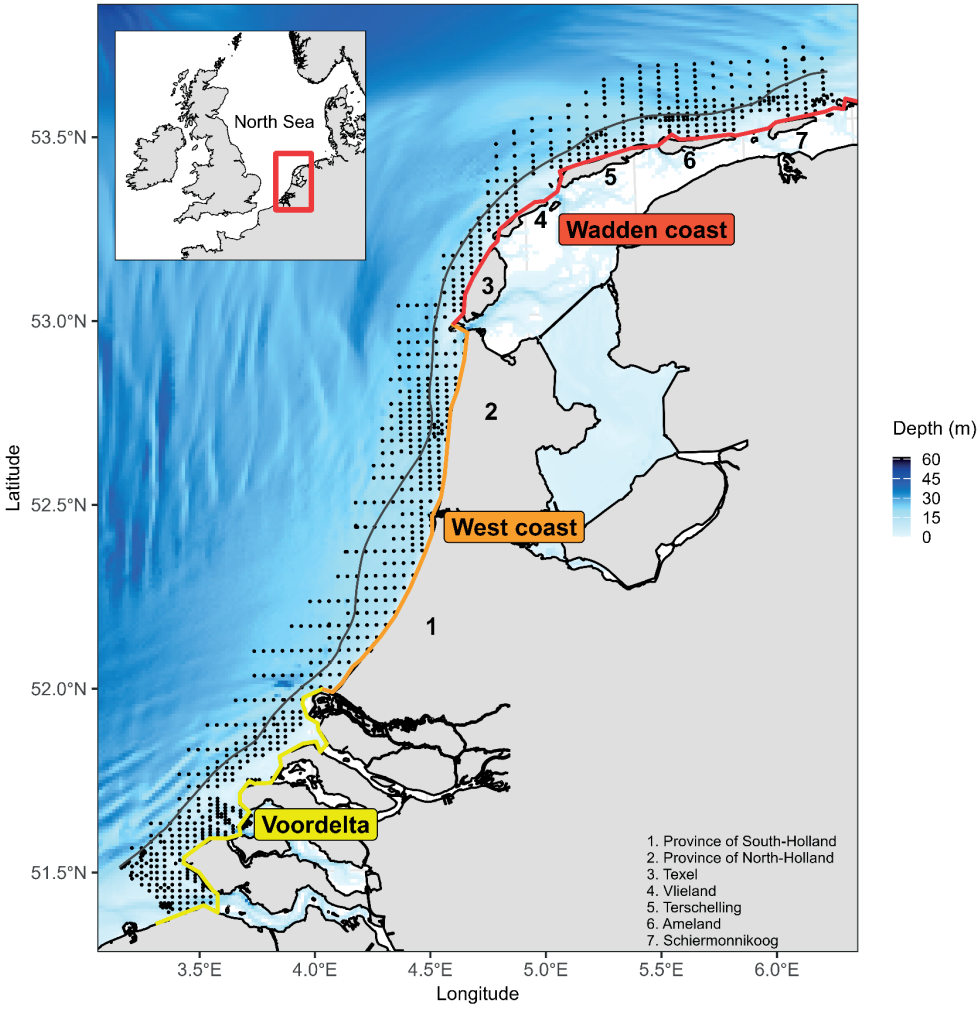


Figure S1: Map of the study area along the Dutch coast showing sampling points (black dots) and bathymetry. Three coastal regions are highlighted by color: Voordelta (yellow), West coast (orange), and Wadden coast (red). Numbers indicate two provinces and the Wadden Islands. The smoothed 20 m depth contour is shown in black.

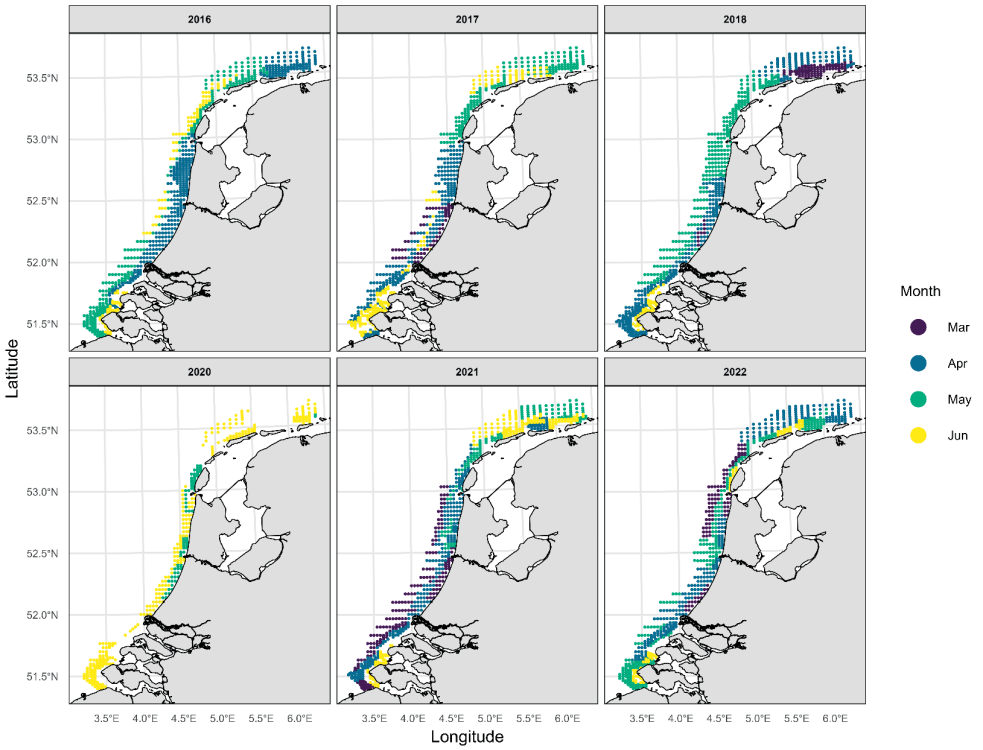


Figure S2: Sampling locations of the Dutch shellfish survey for each year colored by month

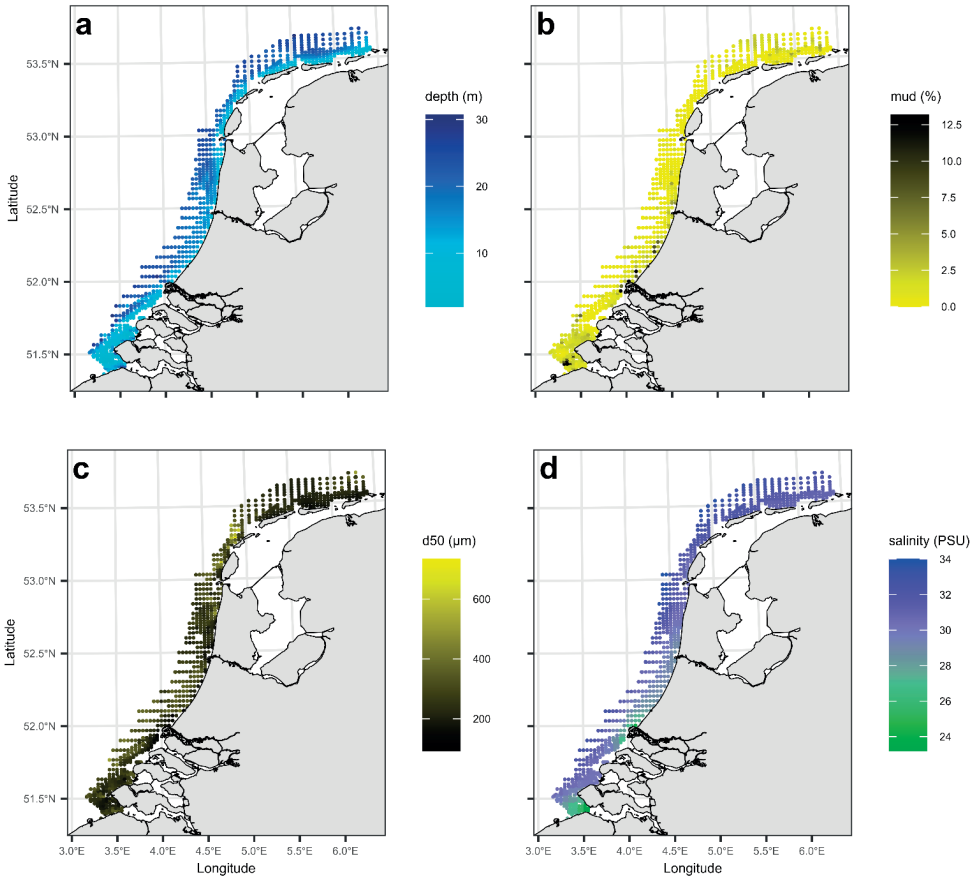


Figure S3: Environmental variables (excluding the benthos biomass metrics) used in the analysis, including (a) depth, (b) mud content, (c) median grain size, and (d) salinity.

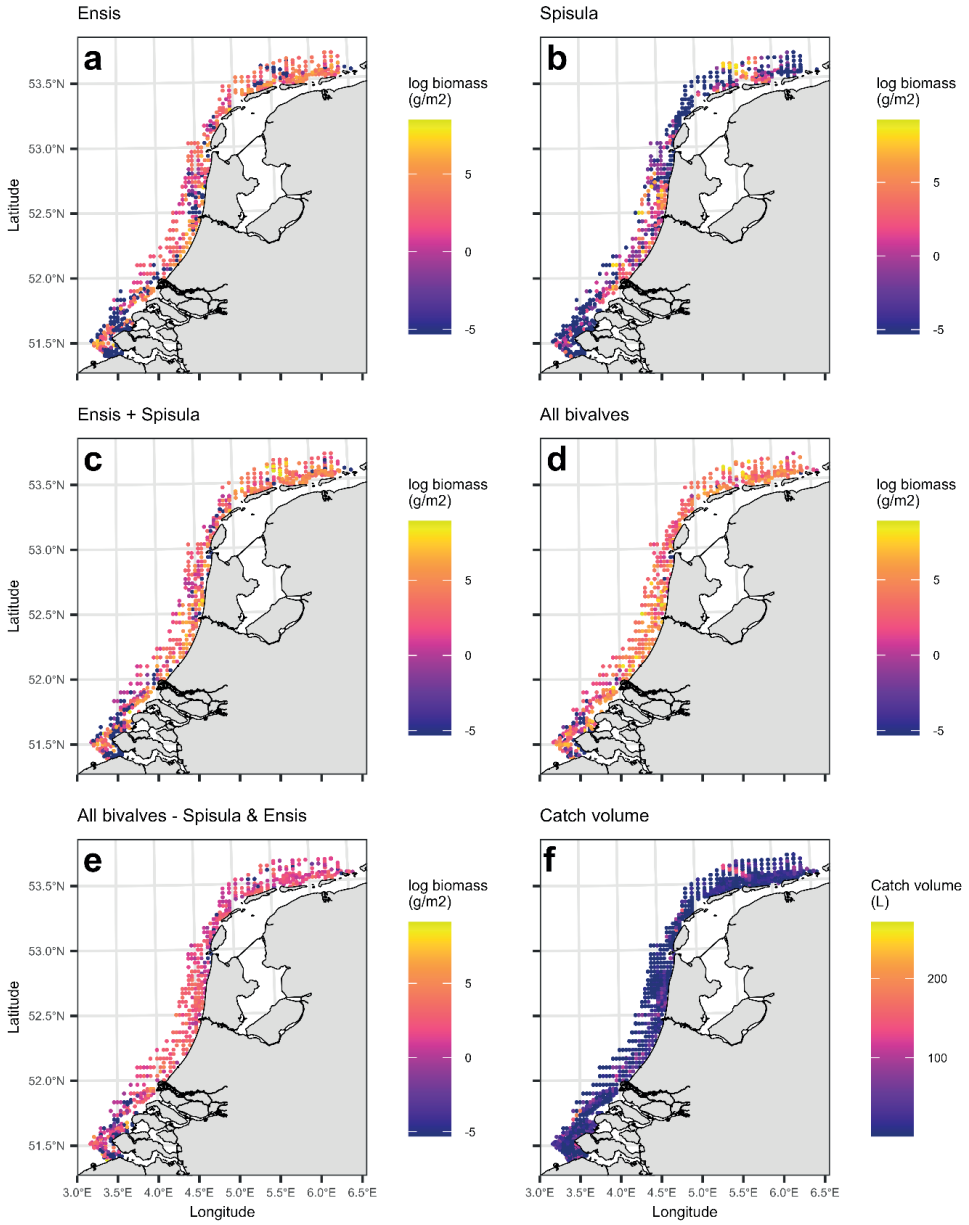


Figure S4: Spatial distribution of the 6 different bivalve metrics (a-f) used in the analysis.

Table S1: Relative contributions of shell species across the six sampling years of the WOT survey.

Species	relative_contribution (%)
Spisula subtruncata	54.34
Ensis Leei	34.12
Limecola balthica	3.49
Abra alba	2.15
Venerupis corrugata	2.05
Donax vittatus	1.18
Chamelea striatula	0.73
Tritia reticulata	0.5
Spisula solida	0.32
Macoma balthica	0.31
Fabulina fabula	0.28
Euspira catena	0.18
Nassarius reticulatus	0.11
Nassarius nitidus	0.04
Spisula elliptica	0.04
Tritia nitida	0.04
Mactra stultorum	0.03
Crepidula fornicata	0.02
Macomangulus tenuis	0.02
Tellina fabula	0.02
Euspira nitida	0.01
Mytilus edulis	0.01
Petricolaria pholadiformis	0.01
Abra prismatica	0
Acanthocardia echinata	0
Aequipecten opercularis	0
Buccinum undatum	0
Cerastoderma edule	0
Corbula gibba	0
Diplodonta rotundata	0
Dosinia exoleta	0
Epitonium clathrus	0
Gari fervensis	0
Laevicardium crassum	0
Littorina littorea	0
Mya truncata	0
Phaxas pellucidus	0
Ruditapes philippinarum	0
Striarca lactea	0

Table S1: Continued.

Species	relative_contribution (%)
Tellimya ferruginosa	0
Tellina tenuis	0
Thracia phaseolina	0
Varicorbula gibba	0

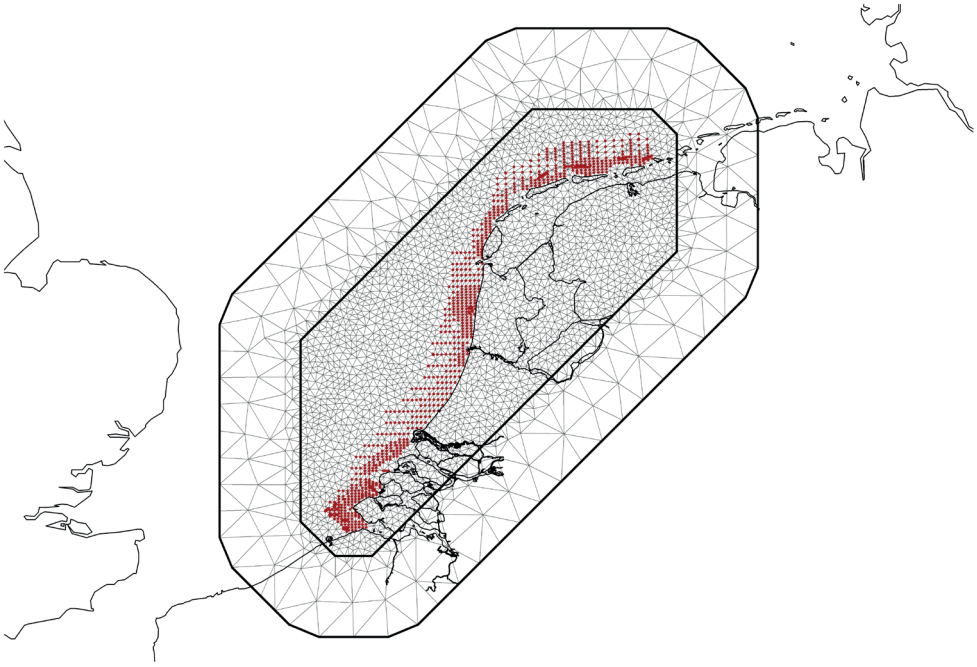


Figure S5: The used mesh for the INLA models. Red dots are sampling locations analysed in this study.

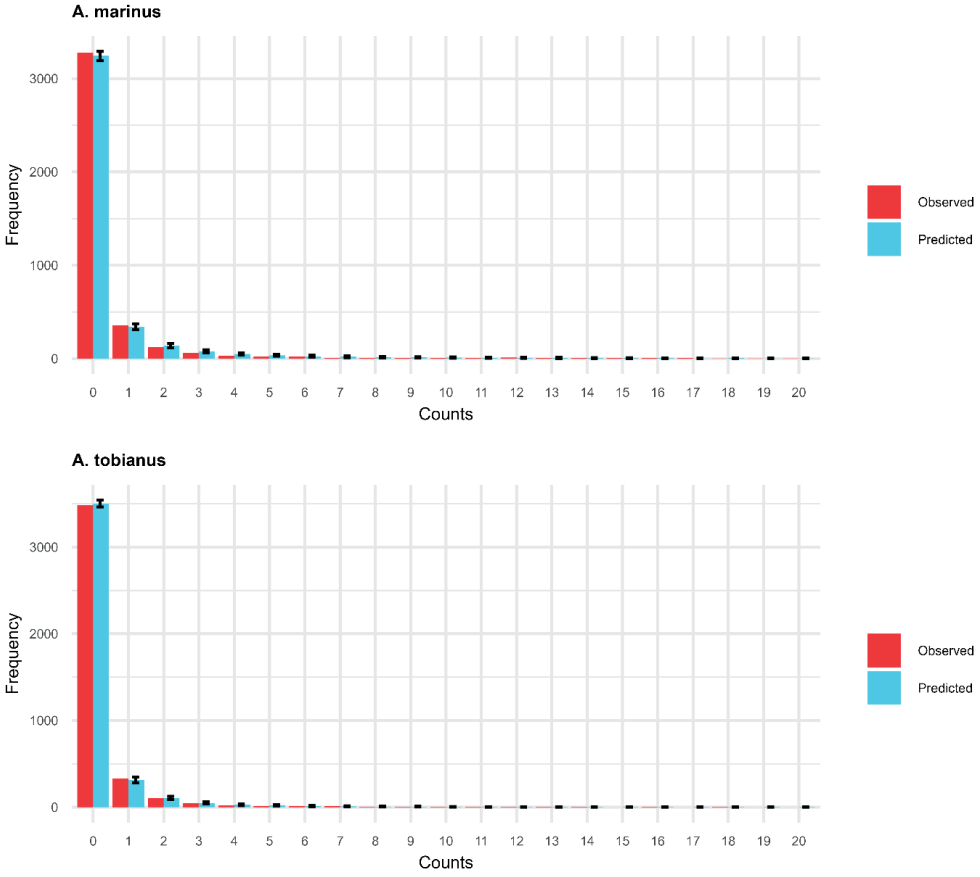


Figure S6: Comparison of observed and (rounded) predicted counts from the best-performing model (Base + all_bivalves + depth + salinity). Error bars represent 95% uncertainty intervals based on (100) posterior simulations. Only counts up to 20 are shown. Top panel A. marinus, bottom panel A. tobianus.

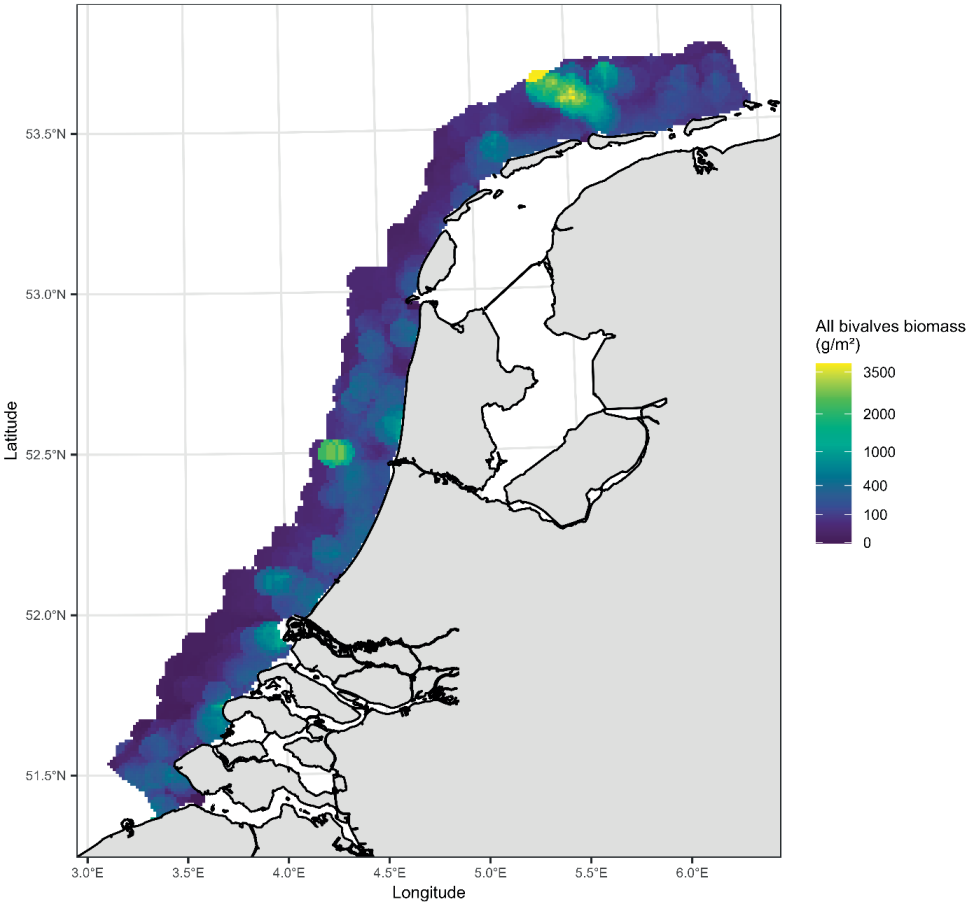


Figure S7: Spatial distribution of bivalve biomass used as a predictor in the model. Values represent the mean biomass from all six WOT survey years, calculated within a 5 km radius around each grid cell.

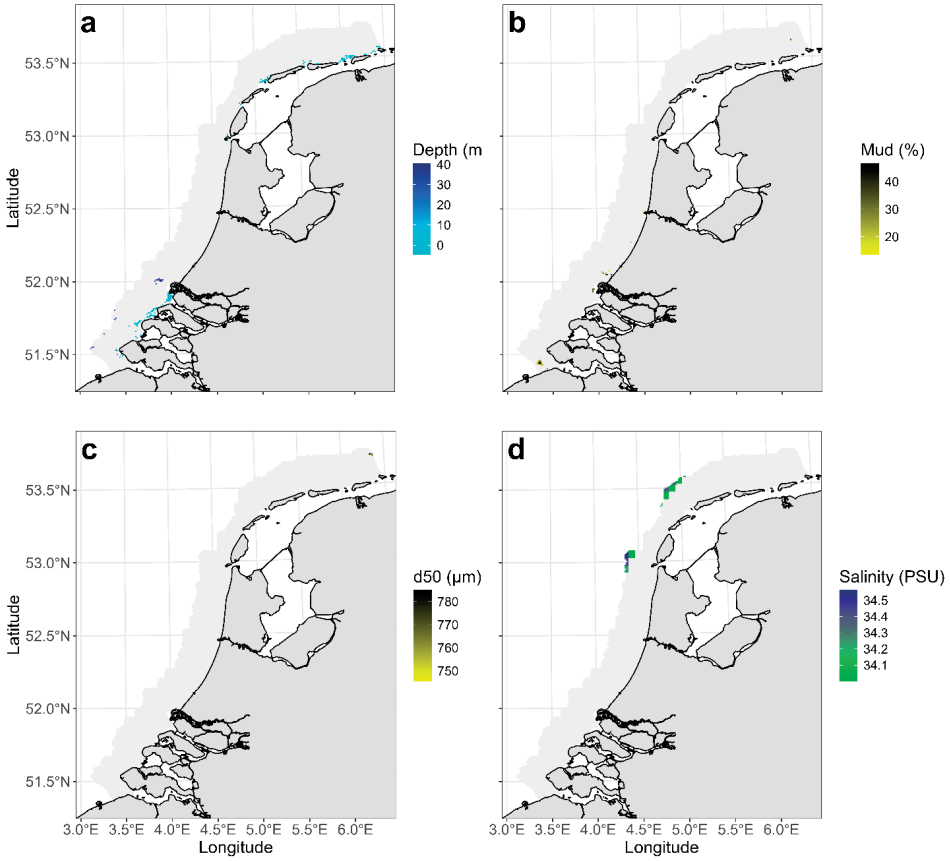


Figure S8: Areas where environmental conditions fall outside the observed range used for model fitting. a) Depth includes very shallow (negative) values as well as localized deeper areas. b) Small, localized regions exhibit higher mud content (>14%) and c) median grain size (d50; >733 µm) than observed at the sampling locations. d) Salinity values are higher than the sampled locations towards the offshore edges of the prediction grid. Bivalve predictors are not shown, as they are derived directly from sampling locations and therefore do not extend beyond the observed range.

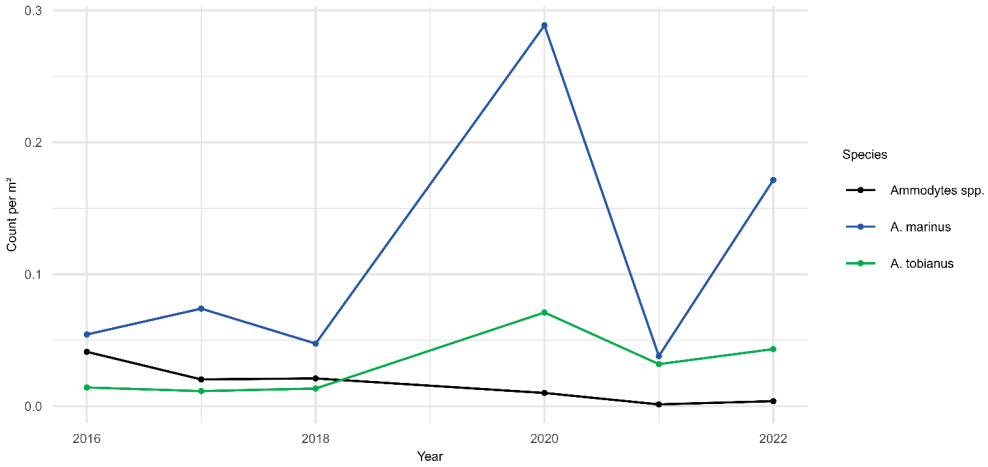


Figure S9: Observed annual sandeel densities per species in the WOT shellfish survey.

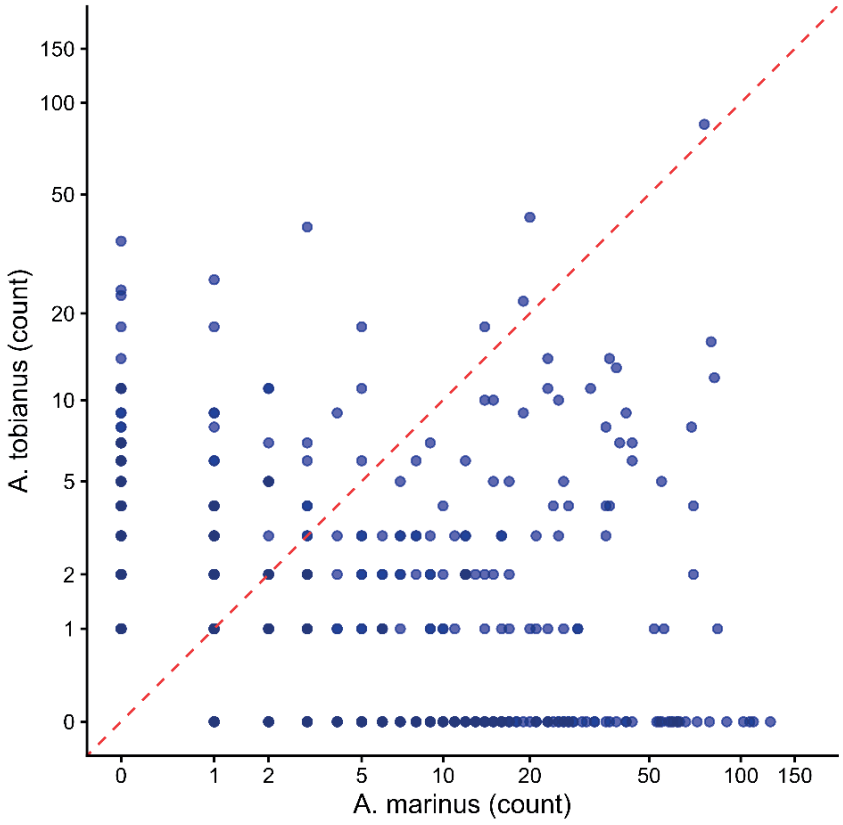


Figure S10: Observed counts of each *Ammodytes* species at sampling stations where at least one of the two species was recorded.

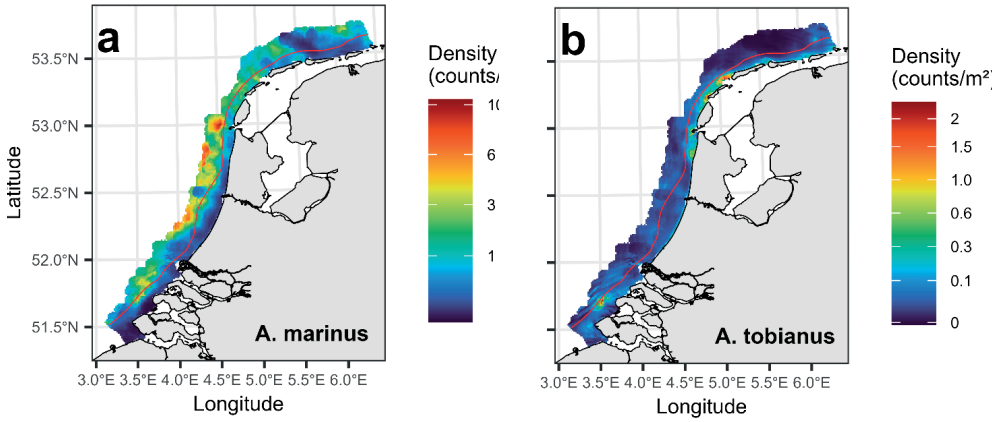


Figure S11: Predicted distribution (in counts per m2) of both *Ammodytes* species along the Dutch coast at sunset (relative time-of-day = 1.0). The smoothed 20 m depth contour is shown in red.

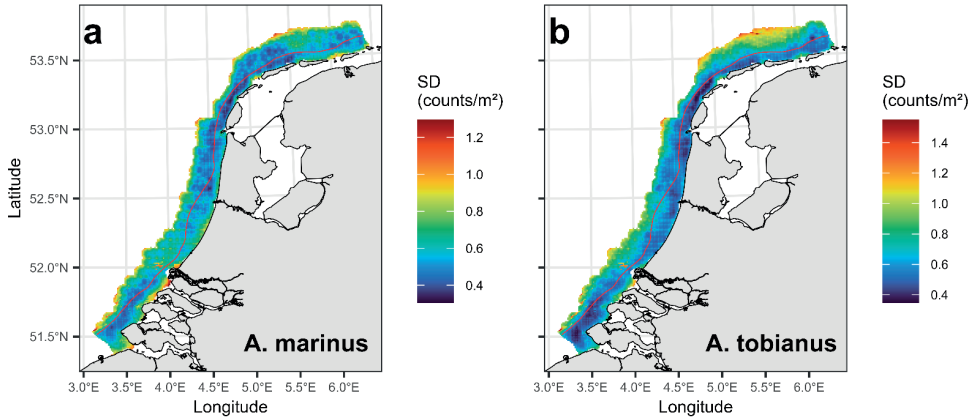


Figure S12: Spatial distribution of prediction uncertainty, expressed as the posterior standard deviation (SD).

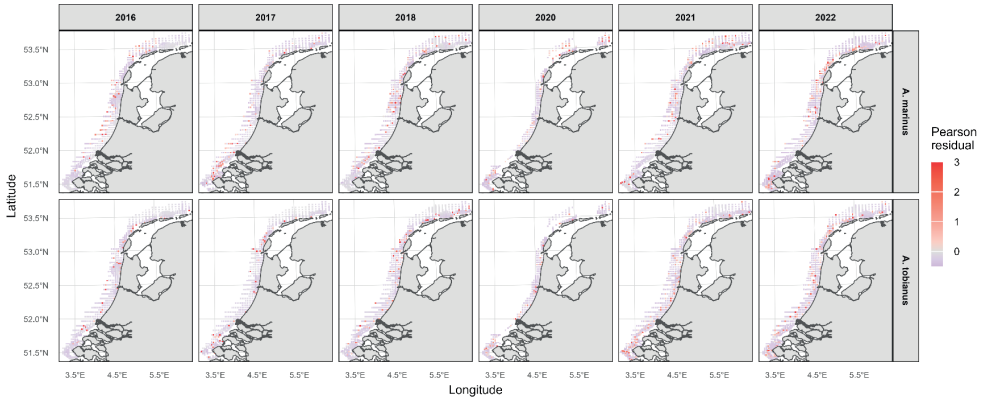


Figure S13: Pearson residuals of the best model (including salinity, depth, biomass as explanatory variables) per year.

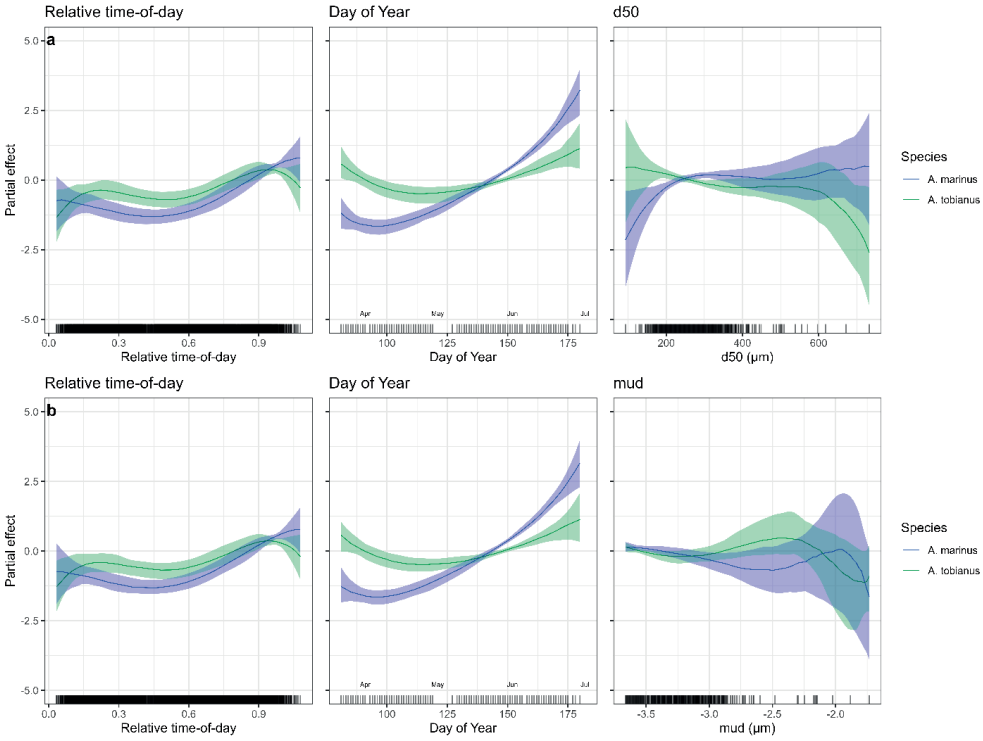


Figure S14: Estimated partial effects (on the log scale) of environmental variables from models including a) median grain size and b) mud content (on the logit scale).

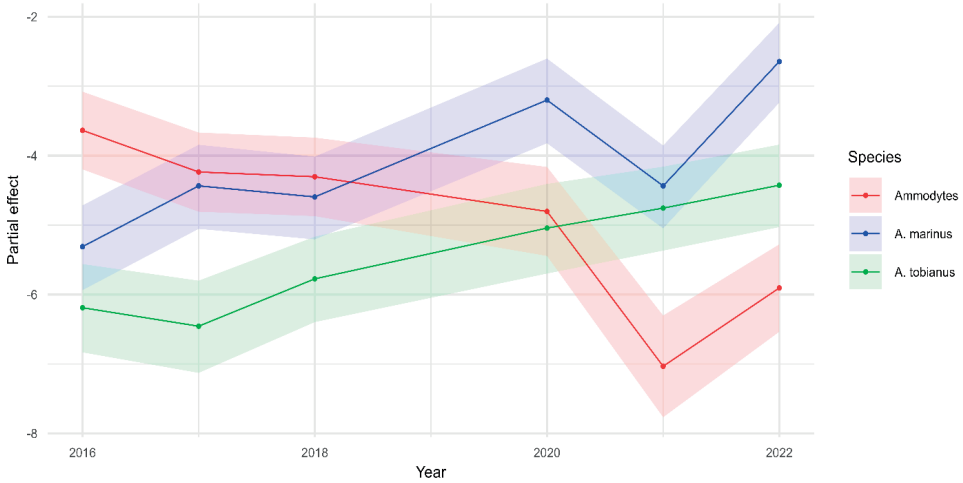


Figure S15: The estimated species-specific fixed year effect (log scale) of the best model (including salinity, depth, biomass as explanatory variables).

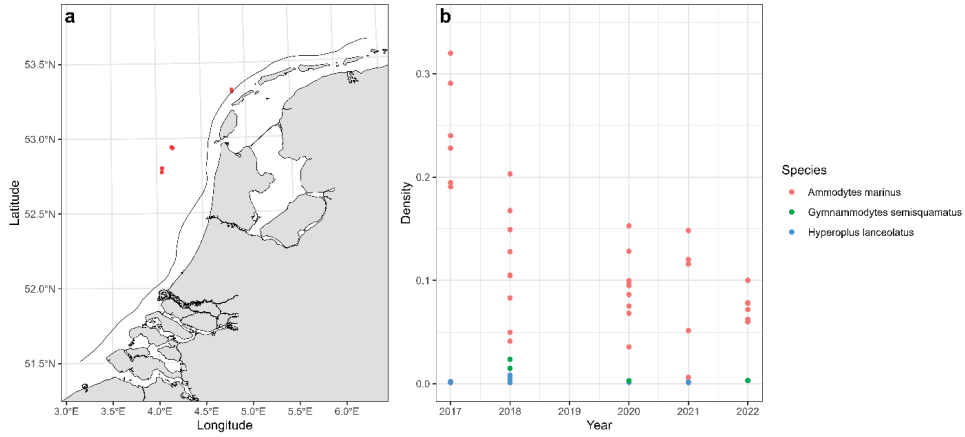


Figure S16: a) The geographical locations of the sampling points. b) Observed sandeel densities from the North Sea Sandeel Survey (NSSS) during 2016–2022.





6

General Discussion

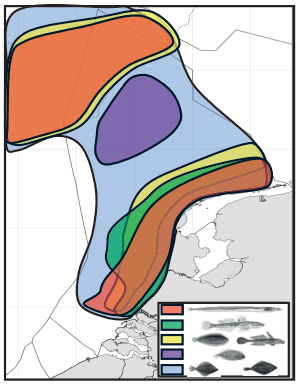
Bram Parmentier

Small (<30 cm) demersal fish, including buried sandeel (despite their usual classification as pelagic species), play an important role as prey for a wide range of predators in the southern North Sea, such as marine mammals, seabirds, and piscivorous fish. However, significant knowledge gaps remain in species-specific spatial distribution, abundance, energetic characteristics, and diurnal behaviour. Therefore, the primary objective of this thesis is to improve the understanding of these key aspects of prey availability. Accordingly, the main research question guiding this thesis is: **What are the distributional, energetic, and (diurnal) behavioural characteristics of small demersal fish, particularly the two *Ammodytes* species, in the southern North Sea?** This main question is addressed through the following sub-questions:

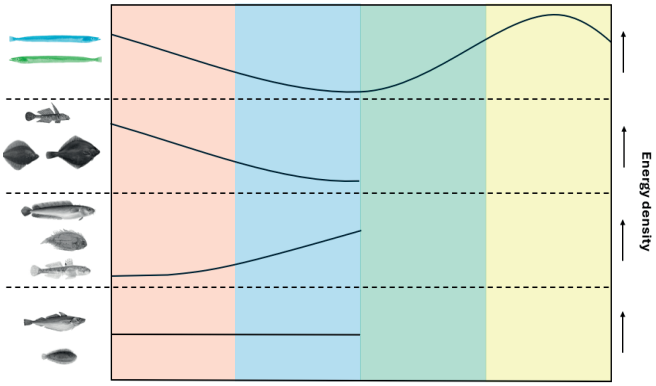
- What are the spatial distributions, in terms of both biomass and energy density, of the most abundant small demersal fish, as well as of the entire aggregation of all small demersal fish?
- Do the two *Ammodytes* species play different roles as prey in the ecosystem?
    - Which factors affect their spatial distributions and do they differ?
    - Do they exhibit different vertical migratory behaviours, either during the day or throughout the foraging season?
    - Do they differ in energy content throughout the season?

In this final chapter, I synthesise the results of the previous chapters (see Fig. 1) and highlight the main findings. I further provide recommendations for future research and discuss the potential (management) applications of these findings.

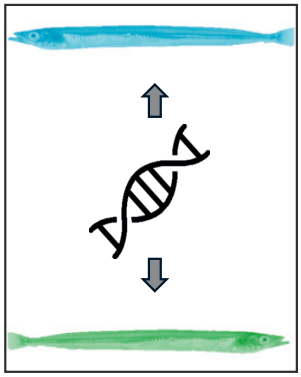
Chapter 2
Distributions of small demersal fish



Chapter 3
Seasonal energy densities



Chapter 4
DNA separation *Ammodytes* species



Chapter 5
Ammodytes-specific seabed distribution and and diurnal behaviour

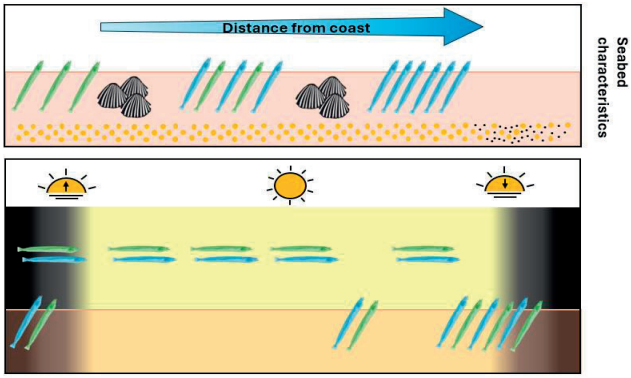


Figure 1: Visual overview of the topic and main outcomes per chapter. The colour of sandeel indicates which species it is: grey = Ammodytidae (unidentified), blue = A. marinus, and green = A. tobianus.

1. PREY AVAILABILITY IN SPACE

Spatial distribution of prey is a key determinant of predator–prey interactions, as predators must encounter prey in order to consume them. Consequently, understanding the spatial distribution of prey is essential for interpreting predator foraging behaviour. The southern North Sea is an area where small demersal fish are particularly abundant (Callaway et al., 2002). However, detailed information on the (absolute) spatial distributions of small demersal fish, and particularly sandeel, has remained limited due to the difficulty of quantifying them through standard annual fish surveys (see **Chapter 1** for more details). To address this gap, this study used alternative sampling gears originally developed for macrobenthic sampling: the Netherlands Institute of Sea Research (NIOZ) Triple-D dredge and the dredge used in the WOT (Statutory Research Tasks) shellfish survey carried out by Wageningen Marine Research (WMR). The advantage of these dredges is that they sample within the seabed and use fine mesh sizes (WOT: 10 cm sampling depth and 5×5 mm mesh; Triple-D: 20 cm sampling depth and 7×7 mm mesh), allowing efficient sampling of small demersal fish, including sandeel, even when they are buried in the sediment.

Chapter 2 examines the spatial distribution of small demersal fish in the Dutch North Sea and the UK Dogger Bank based on Triple-D data. Biomass distribution maps were created for the seven most abundant species (dab, dragonet spp., goby spp., plaice, sandeel spp., scaldfish, and solenette), as well as for all species combined. The observed distribution patterns corresponded with (historically) described large-scale patterns (Fonds, 1973; Heessen et al., 2015; van der Veer et al., 1990; van Hal et al., 2010). For sandeel (Ammodytidae) published distribution patterns have been inferred from commercial fishing grounds (Jensen et al., 2011), providing presence–absence information of (foraging) sandeel. The sandeel fishing grounds correspond to some extent with our observed distribution of (buried) sandeel (Fig. 2). For example, both indicate little to no sandeel presence in the Oyster Ground area, while some sandeel-identified areas along the coast overlap. However, our results suggest that buried sandeel along the Dutch coast are more widely dispersed than indicated by fishing grounds alone. This may indicate that sandeel aggregate to specific areas during foraging. Another difference between our sandeel distribution and those indicated by sandeel fishing grounds is that the extensive fishing grounds at the Dutch Dogger Bank are not well reflected in our data. These differences in sandeel distributions are probably due to methodological differences between studies, such as sampling buried versus foraging (water-column) individuals, as well as seasonal differences (winter versus spring/summer). In addition, the distribution of fishing grounds is likely influenced by factors beyond sandeel

abundance. These include shipping lanes and human infrastructure (e.g. wind farms and oil and gas platforms), where fishing activities are restricted.

Recently, a new study also mapped sandeel (*Ammodytes marinus*) distribution in the North Sea based on data from annual ICES bottom trawl surveys (Benaksas et al., submitted). The absolute magnitude of biomass estimates differed substantially between the studies, as expected given the low catchability of sandeel in trawl surveys (Knijn et al., 1993). For instance, Benaksas et al. reported a mean biomass of 0.00048 g m^{-2} (maximum: 0.0024 g m^{-2}), compared with our estimated mean of 0.47 g m^{-2} (maximum: 7.41 g m^{-2}) at the same spatial resolution in overlapping areas of the Dutch Economic Exclusive Zone (EEZ) (Fig. 2). In contrast, spatial patterns were broadly comparable between our study and Benaksas et al., although with some differences at a more local scale: our estimates indicated relatively high biomass near the two westernmost Wadden Islands (Texel and Vlieland), whereas Benaksas et al. predicted higher (relative) biomass in the Dogger Bank area and the southern part of the Dutch EEZ.

One possible explanation for the difference in relative patterns between Benaksas et al. and our study in Chapter 2, particularly the relatively high abundance observed along the western Wadden Islands (Fig. 2D), is that, unlike their analysis, our study also included the more coastal species *Ammodytes tobianus*. This is because sandeel in the earlier years of the Triple-D dataset were not identified to species level, as *Ammodytes* species are difficult to distinguish morphologically (Heessen et al., 2015; Nævdal et al., 2002). In addition, specimens were often damaged (approximately 30% by weight), which further hindered morphological identification. This damage is likely caused by sandeel attempting to escape but being unable to avoid the dredge's cutting blade as it penetrates the seabed.

Similarly, a substantial proportion of sandeel specimens in the WOT annual shellfish data were also damaged (approximately 50%). To enable identification of these individuals and to validate morphological identification, species-specific primers for real-time PCR DNA identification of the *Ammodytes* species were developed, as described in **Chapter 4**. The DNA method facilitated analyses of *Ammodytes*-specific small-scale distribution patterns in **Chapter 5**. The analysis in Chapter 5, based on the WOT shellfish data from the Dutch coastal area (<20 nm), showed a general spatial separation between the two *Ammodytes* species. Hotspots of *A. marinus* were found in deeper waters, while *A. tobianus* was more abundant in shallower areas. Our findings are consistent with previous localised studies in the Dutch EEZ that examined species-specific habitat preferences of sandeel species (Tien et al., 2017; van Hal et al., 2021). However,

we also found that the *Ammodytes* species co-occurred, including within the same sampling hauls. This was particularly in 2022, when *A. marinus* occurred closer to the coast than in other sampling years, resulting in greater spatial overlap between the species. Such spatial overlap suggests that the species are not strictly segregated and share seabed habitat preferences. Similar spatial overlap in sandeel species occurrence has also been observed elsewhere, for example in Denmark (van Deurs et al., 2012). The results further indicated that sandeel spatial patterns were influenced by bivalve distribution, as both species were negatively associated with bivalve biomass. We hypothesise that sandeel avoid these areas because dense bivalve assemblages may hinder burrowing behaviour, similar to the avoidance of gravel-rich sediments (Henriksen et al., 2024; Holland et al., 2005). The improved knowledge of the distribution of small demersal fish, particularly the two most abundant sandeel species, help improve our understanding of foraging behaviour of predator species in the Dutch North Sea.

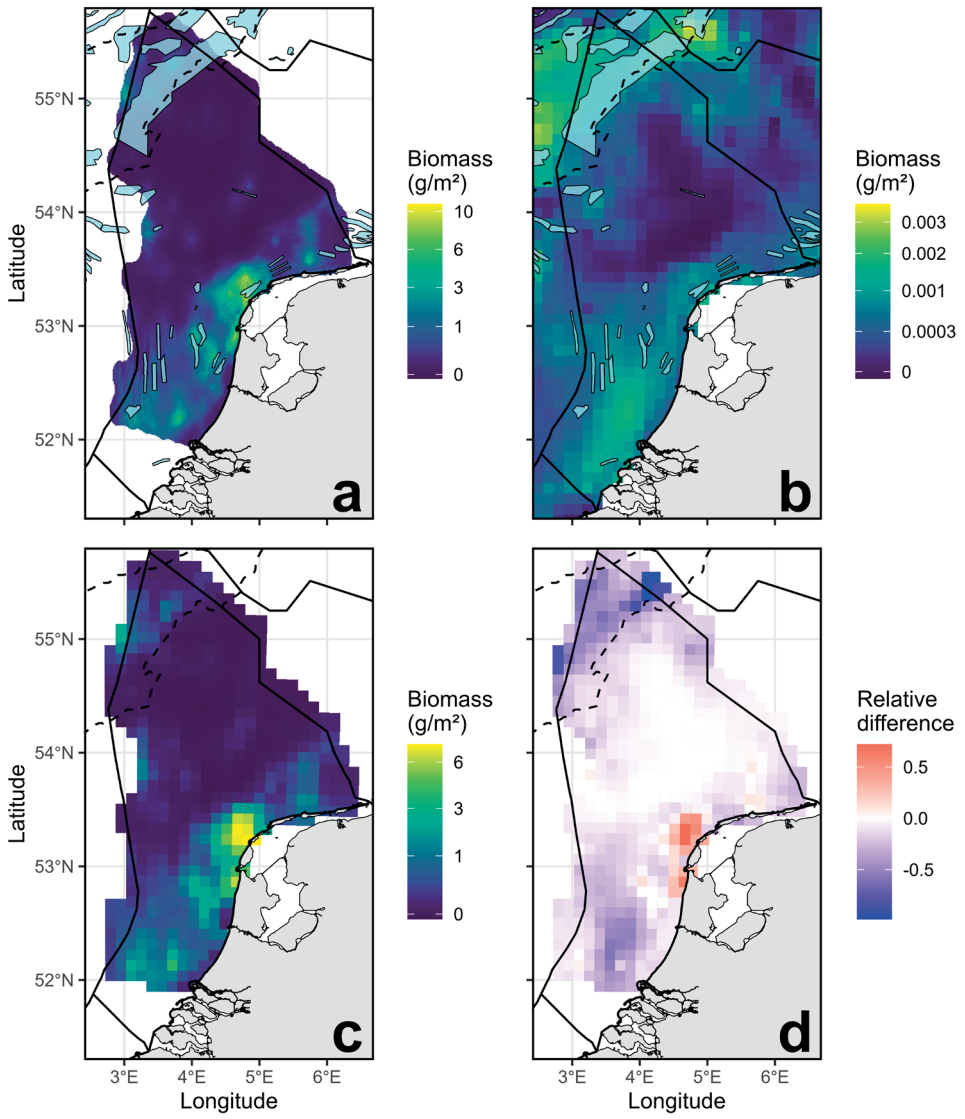


Figure 2: a) Seabed sandeel distribution based on Triple-D (Chapter 2) including sandeel fishing grounds from Jensen et al. (2011). b) Sandeel distribution by Benaksas et al. (Submitted). c) Sandeel distribution of Chapter 2, in a lower resolution for comparison to Benaksas. d) Relative differences in spatial distribution between panels b and c.

2. PREY AVAILABILITY IN TIME

Prey availability also has a temporal component, both in terms of energy density and abundance. In **Chapter 2**, we found that small demersal fish biomass was particularly high in early autumn, reaching up to three times higher values than at other times of the year. This pattern is likely driven primarily by fish growth, as well as the recruitment of new cohorts reaching size classes large enough to be effectively captured by the sampling gear.

Different seasons further influenced energy densities. In **Chapter 3**, we found that seasonal trends from early winter to early spring were species-specific. Energy density (kJ g^{-1} wet weight) declined over winter for dab, dragonet, plaice, sandeel, and sole. In contrast, rockling, scaldfish, and gobies increased from early autumn to early winter before declining. Energy densities of solenette and whiting remained relatively stable during this period. In absolute terms, whiting consistently showed low energy density over the whole measuring period, consistent with its classification as a low-quality prey species (Pedersen et al., 2001). Gobies have also been identified as relatively low-energy prey (IJsseldijk et al., 2021), however our results suggest that this generalisation may overlook temporal variation, as in early spring their weight-specific energy densities exceeded those of sandeel, which are generally considered high-energy prey (Wanless et al., 2018). We further used the species-specific and seasonal energy densities to convert biomass estimates from Chapter 2 into species-specific and total energy landscapes. This step is essential because the energetic quality of prey, potentially even more important than prey quantity, plays a key role in shaping predator foraging strategies (Spitz et al., 2012).

Another important factor for its availability to predators is the diurnal behaviour of sandeel. Seabird species such as sandwich terns capture sandeel only in the water column (Baptist & Leopold, 2010), whereas harbour porpoise appear to target buried sandeel (Schneider von Deimling et al., 2023). Therefore, sandeel availability to predators depends not only on their spatial distribution and absolute densities but also on their diurnal behaviour. In **Chapter 5**, we found that both sandeel species emerge from the sediment early in the day, with a substantial proportion already in the water column before sunrise. From the afternoon onwards, they gradually returned to the sediment. This pattern is consistent with observations of *A. marinus* in Norwegian waters (Komiyama et al., 2024). To my knowledge, our study is the first to investigate species-specific variation in sandeel diurnal behaviour within the same area. The importance of sandeel diurnal behaviour for prey availability is reflected in predator species behaviour. For example, in sandwich tern chick provisioning, the proportion of

sandeel delivered to chicks gradually declined throughout the day (Stienen et al., 2000). Conversely, the proportion of sandeel in stomach contents of haddock and whiting increased rapidly during the night (Temming et al., 2004). Both observations are consistent with our results regarding the diurnal pattern in availability of sandeel in the water column versus the seabed.

Sandeel diurnal behaviour has a seasonal component (Macer, 1966). In spring, sandeel progressively emerge from the sediment, with the timing and magnitude of the peak varying by location and year, typically reaching a maximum in late April to mid-May (Henriksen et al., 2021). This is followed by a gradual decline as feeding activity ceases, resulting in a bell-shaped curve in relation to time of year and water column presence (Henriksen et al., 2021; Komiyama et al., 2024). For *A. tobianus*, we observed a similar but reversed pattern, as our sampling was conducted in the seabed, with lowest abundances in early May (**Chapter 5)**. In contrast, *A. marinus* showed steadily increasing densities in the seabed, suggesting a continuous decline in water column presence from late March to early July. However, these observed patterns are likely largely driven by the growth of the age-0 cohort of *A. marinus* into size classes that are more effectively captured by the dredge, rather than reflecting behavioural changes. The seasonal effect on diurnal behaviour appears to be reflected in seal diving (foraging) behaviour. During the summer months, seals showed clear diurnal diving patterns, with most diving activity occurring in the early morning and late afternoon, coinciding with periods when sandeel either emerge from or return to the sediment. In winter, this pattern was not observed (Windels et al., 2026). Overall, temporal variation strongly influences prey availability through seasonal changes in biomass, energy density, and sandeel distribution between the seabed and water column, thereby affecting prey accessibility for predator species.

3. SPECIES-SPECIFIC ECOLOGICAL ROLES OF *AMMODYTES*

An overarching goal for this thesis was to assess whether the two most abundant *Ammodytes* species in the Dutch coastal zone differ in their ecological role as prey within the ecosystem.

The spatial distribution patterns differed between the two *Ammodytes* species. Along the Dutch coast, the highest seabed densities of *A. tobianus* generally occurred in waters shallower than the 20 m depth contour. Hotspots of *A. marinus* were found predominantly in deeper areas beyond this depth (**Chapter 5**). In addition, mean densities differed between species, with

A. marinus reaching higher densities (2.1 individuals m^{-2}) than *A. tobianus* (0.7 individuals m^{-2}). Optimal foraging theory suggests that predators feeding on sandeel should target high-density *A. marinus* hotspot areas. However, for central-place foragers—predators that must return to a resting site or breeding colony—distance to feeding areas is an important factor in their foraging strategy (Olsson et al., 2008). This is particularly relevant for single-prey-loading predators, which transport only one prey item at a time (e.g. sandwich terns; Stienen et al., 2000). For such predators, despite the lower density, the shorter travel distance to *A. tobianus* habitats may result in *A. tobianus* being a more accessible prey item. Moreover, high-density *A. marinus* areas along the Holland coast (North and South Holland) may lie at the edge of the foraging range of some central-place foragers, such as seabirds breeding in coastal colonies with a range of 27 km (Fijn et al., 2017).

For species-specific diurnal behaviour, no differences between the two species were found (**Chapter 5**). This indicates that the species do not appear to differ in their availability to seabed- or water column–associated predators at specific times of day. Therefore, it is unlikely that predators target a particular *Ammodytes* species based on time of day alone. In contrast, the decreased appearance in the water column over the season of *A. marinus* could influence predator diet. However, as discussed in the previous temporal section, the observed differences in density in the course of the season may not reflect seasonal differences in diurnal behaviour between the two species but rather be caused by the growth of age-0 group *A. marinus*.

For weight-specific energy densities, also no differences were found between the two species (**Chapter 3**). Thus, body size, rather than energy density is proposed as a key determinant of total energy. Differences in body size distributions between the two species were observed (**Chapter 5**). *A. tobianus* exhibited a wider length distribution (between 5-20 cm), whereas *A. marinus* showed more distinct cohorts with a relatively narrow size range. This may imply that *A. marinus* represents a more variable resource for predators with a clear size preference. For instance, incubating sandwich terns in the southern part of the Netherlands were found to consume mainly 8–14 cm sandeel (Courtens et al., 2017). In some years (e.g. 2020–2023), this size class was widely available in *A. marinus* populations, whereas in 2016 mainly larger individuals were available. However, it remains unclear whether this apparent size preference reflects active prey selection or simply prey availability.

To summarize, the results show that the two *Ammodytes* species in the Dutch EEZ do not differ in energy density or diurnal behaviour, but do differ in their

spatial accessibility due to nearshore versus offshore distribution patterns. However, current evidence is insufficient to determine whether the two species play different ecological roles in the system. This study nevertheless provides a foundation for future research on *Ammodytes*-specific predator–prey relationships, particularly if *Ammodytes* species are determined at species-level in predator diet studies.

4. ABSOLUTE FISH DENSITIES

The standard ICES fish surveys have as their main objective to provide biological data for stock assessments and to detect changes in the distribution and relative abundance of commercially important fish species (ICES, 2022). However, in addition to relative abundance, absolute abundances are as relevant in marine ecology, estimates have long been a key objective in marine ecology, as it influences carrying capacity for predator species, the comparative quantification of impacts by fishery and natural predators (Aarts et al., 2019; Furness, 1990; Walker et al., 2017). Absolute abundances can be derived from relative abundance estimates by correcting for gear efficiency, defined as the proportion of fish present in the fishing path that is captured. Gear efficiency (or gear catchability) depends on several factors, including gear type, fish species, fish size, and environmental conditions (e.g. turbidity or water temperature) (Fraser et al., 2007; ICES, 2004).

For small demersal fish, two main issues arise. First, small fish, particularly sandeel, have a low probability of being captured by standard annual survey gear (ICES, 2004; Knijn et al., 1993). Low catchability can result in so-called "false zeros," where an observed absence may be caused by gear inefficiency rather than a true absence of fish. Consequently, low catchability reduces the reliability of the observations (ICES, 2004). Second, species-specific catchability rates are largely unknown, so assumptions are required. Low catchability and uncertainty in species-specific catchability values introduce substantial uncertainty into both relative and, particularly, absolute abundance estimates.

The substantially higher (at least twofold) observations from the Triple-D compared to standard surveys (see Chapter 2 and Fig. 2) suggest higher catchability of the Triple-D gear and therefore relatively reliable observations for small demersal fish, including sandeel. However, catchability rates of the Triple-D also remain unknown. For instance, it is unclear how the limited width (20 cm) of the cutting blade and cage opening influences catch efficiency.

Absolute abundances therefore cannot be estimated. Nevertheless, the uncorrected values can be interpreted as conservative minimum estimates.

Every sampling gear targets specific size classes, generally involving a trade-off between effectively sampling larger versus smaller individuals, with mesh size being an important factor. Small mesh sizes are more suitable for capturing small fish, but can also create net clogging, potentially allowing larger fish to escape. Using body size–abundance scaling relationships, we roughly assessed which size classes are most accurately sampled by the Triple-D dredge compared to a GOV otter trawl (Box 1).

Box 1: Size spectrum. Size spectra represent the general relationship between log body size (often expressed in body mass) and log abundance in an ecosystem, typically following a negative scaling relationship described by a power law. This negative slope arises because energy availability decreases with increasing trophic level and body size, as energy is lost at each step of the food web through metabolic processes and inefficiencies in energy transfer between prey and predator. As a result, ecosystems generally contain many small organisms and progressively fewer large organisms (Brown et al., 2004). A size spectrum therefore provides an overview of how energy is distributed across size classes. By comparing size spectra and their associated power-law relationships over time, it is possible to gain insight into which parts of the system are over- or under-represented, which hint at overexploitation of specific size classes (Jennings & Blanchard, 2004; van Langevelde et al., 2020).

Only four log body mass classes overlapped (1.95, 2.25, 2.55, and 2.85) between our dataset and Jennings and Blanchard's (2004) (Fig. 3). When comparing biomass densities, the smallest body mass class is higher in the Triple-D data, the two intermediate classes are very similar between gears, and the largest class is higher in the GOV otter trawl dataset. These differences illustrate gear-specific capture efficiency: smaller (lighter) fish are better represented in the Triple-D survey relative to their abundance in the GOV trawl, whereas larger (heavier) fish are better represented in the GOV trawl. Triple-D biomass densities in the log body mass classes below 1.65 do not follow the expected power-law relationship (−1 slope). This likely reflects that biomass and energy in the smallest body mass classes are increasingly dominated by non-fish organisms, such as zooplankton and other invertebrates.

The comparison illustrates that fishing gears sample only a specific component of the fish community effectively, i.e. with high catchability. Therefore, combining datasets from different gear types is essential to obtain a complete picture of the overall fish community, as different gears reflect trade-offs in sampling efficiency between pelagic and demersal species as well as between small and large fish

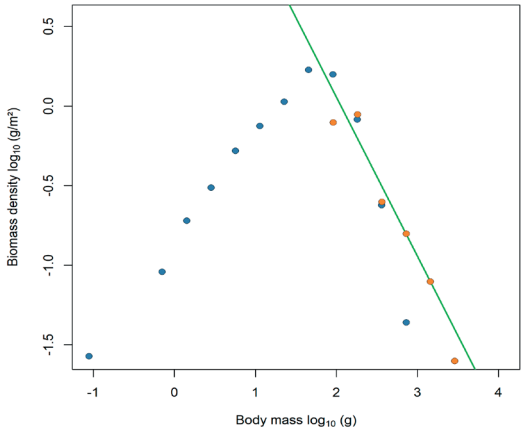


Figure 3: Size spectrum of North Sea fish from Jennings and Blanchard (2004). Orange dots represent their catchability uncorrected observations, with the green line showing the fitted linear relationship with a slope of −1. Blue dots show observations from the Triple-D survey.

5. LINKING PREY TO PREDATOR FORAGING

Top predators such as marine mammals and seabirds are valuable indicators for marine ecosystem functioning (Bossart, 2011; Parsons et al., 2008). However, our understanding of the links between these predator species and lower trophic levels, including small demersal fish, remains limited (Madden et al., 2025). This thesis provides insight into different aspects of availability of small demersal fish as prey. A logical next step is to link spatial differences in prey availability to the distribution and foraging movements of predator species, such as marine mammals, seabirds, and predatory fish. This can be achieved by combining the spatial prey distribution maps created in this thesis with animal-tracking data. In the Dutch part of the North Sea, tracking data are available for several predator species, including seal (Carter et al., 2025), porpoise (Vrooman et al., 2024), terns (Fijn et al., 2022) and gulls (van Bemmelen et al., 2025).

Figure 4 shows grey seal tracking data overlaid on the small demersal fish distribution map from Chapter 2. This reveals some overlap between predator movements and prey availability, particularly north of the Wadden Islands. However, other areas show a mismatch, such as the small demersal fish hotspot at 53°N, which is not strongly used by seals, and the coastal area at 52.4°N, where many seal tracking points occur despite little indication of high prey abundance. A detailed analysis, including prey expressed in calorific energy (Chapter 3) and species-specific distributions, could improve our understanding what prey aspects influences predator foraging (grey seal used as an example here). For instance, a clear positive association with a specific prey species or group may indicate that prey characteristics are important, such as spatial predictability (e.g. expected for sandeel) or low escape ability.

A limitation of the approach described above is that predator and prey observations are linked despite not being collected simultaneously. For example, apparent mismatches between predator and prey distributions may result from local prey depletion by predators. Multidisciplinary surveys, such as the cruise conducted at the UK Dogger Bank in summer 2023 (Chapter 2), provide an opportunity to overcome this limitation by observing predators and prey simultaneously at the same location. However, during this specific cruise, predator species were surprisingly low in number and absent at prey hotspots. This was likely due to the record-breaking marine heatwave occurring at the time of the survey (Atkins et al., 2025), although prey availability—particularly of buried sandeel—was high (Chapter 2). Another potential explanation is that unsampled areas may have contained even higher prey densities, with predator species concentrated there instead.

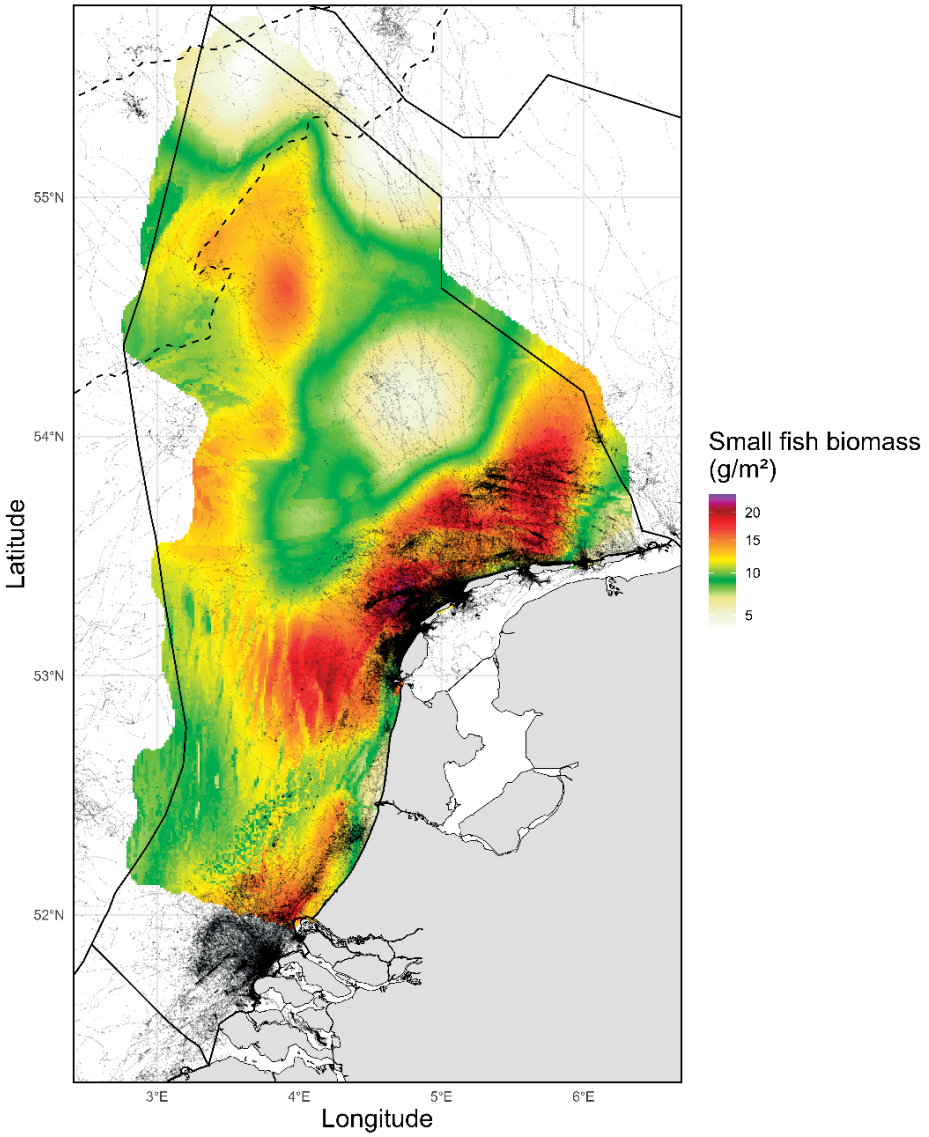


Figure 4: Distribution of small demersal fish (Chapter 2), overlaid with grey seal tagging data (black points) provided by WMR.

6. FUTURE RESEARCH

6.1. Temporal and spatial scales

Due to the lack of a systematic sampling design in the Triple-D data (Chapter 2), temporal trends over the years (e.g. species-specific abundance or distributional changes) could not be examined in detail. In particular, interannual fluctuations, which are typical for short-living species such as sandeel (ICES, 2026b), are key to understand their effects on predator population dynamics. For example, in the UK, low sandeel abundance has been associated with reduced breeding success in several seabird species (Daunt et al., 2008; Régnier et al., 2024). Similar predator–prey relationships are likely to exist in the Dutch part of the North Sea as well. Quantifying species-specific annual variability in small demersal fish is therefore essential to link prey dynamics to predator responses, as it may reveal how variation in prey availability influences predator foraging behaviour, reproductive success, and ultimately population trends. Species-specific changes in the abundance and distribution of small demersal fish within a year could be further explored, as these may influence predator foraging behaviour throughout the year. Seasonal dynamics are well documented for flatfish (Gibson et al., 2002), but remain poorly understood for many other small demersal species.

Regarding spatial trends, we examined spatial distributions at a relatively large scale (covering almost the entire Dutch EEZ or coastal zone). As a result, fine-scale patterns may have been masked by large-scale trends. For example, the large sand dunes in the Brown Bank area are reflected in the estimated sandeel patterns of this study (see Fig. 2A). However, this signal is likely driven by broader depth-related gradients across the entire study area rather than by locally observed patterns, as a low number of Triple-D samples were taken in the Brown Bank. It demonstrates that the spatial scale of analysis influences the patterns that can be detected (Mcgarigal et al., 2016), and that additional studies over a smaller spatial scale are needed to resolve fine-scale environmental effects on the distribution of sandeel and other small demersal fish.

6.2. Sandeel

Given the limited spatial (horizontal) foraging movement of sandeel (Engelhard et al., 2008; Wright et al., 2019), we suggest that densities of buried seabed sandeel are also relevant for their abundance in the water column. However, in the Dutch coastal area, horizontal movements of sandeel may be less constrained, as suitable seabed habitats appear to be widespread. Zooplankton availability may also be more widely distributed in the freshwater-influenced, often non-stratified coastal waters (van Leeuwen et al., 2015), rather than

being concentrated around frontal systems. Therefore, the relationship between seabed occurrence and sandeel foraging locations warrants further investigation in the Dutch coastal area, for instance by using pit tags (see Jørgensen et al., 2017). Beyond horizontal movement, vertical movements of sandeel (see Box 2) also require further study, as previous research has been conducted in deeper, more offshore waters (Freeman et al., 2004; Komiyama et al., 2024). Consequently, sandeel occurrence in shallow water columns (<20 m), such as the Dutch coastal zone, remains poorly understood.

Our results (Chapter 5) indicated that seafloor densities were strongly negatively associated with bivalve biomass. Unravelling whether this is caused by physical blocking or a different sediment preference would benefit from further experimental investigation (see Henriksen et al., 2024), to better understand the underlying mechanisms. Such studies could determine whether the observed relationship is driven by a physical blocking effect, identify potential threshold levels of bivalve biomass, and assess the role of different bivalve species. Additionally, it would be relevant to assess whether the negative spatial correlation between sandeel and bivalve biomass also remains over time. For example, whether years with high bivalve biomass correspond to low sandeel abundance. My hypothesis is that this effect may be limited, as seabed habitat is unlikely to be a limiting factor in the Dutch coastal zone, given that seabed sandeel densities on the UK Dogger Bank were substantially higher than observed in the Dutch coastal zone.

Another important aspect for sandeel predators, particularly for single-prey-loading predators, is sandeel body size. Variation in size should be further investigated at both spatial and temporal scales. At the spatial scale, it is relevant to examine whether different size classes differ in their spatial distribution, as prey size has been shown to influence predator foraging trip distances (e.g. sandwich terns; Fijn et al., 2024). At the temporal scale, diurnal and seasonal foraging dynamics should be considered across size classes. For example, size-dependent differences in daily foraging duration may occur, potentially driven by variation in foraging efficiency, energy requirements or zooplankton availability. Differences between size classes influence size-specific sandeel availability to predators and are likely to propagate through the food web.

Box 2: Sandeel in the water column

Sandeel presence in the water column is of major importance for pelagic predators. To gain more insight into this aspect, a buoy equipped with an autonomous acoustic transceiver (WBAT) system was deployed from late May to mid-October 2024. The WBAT was equipped with 200 and 38 kHz echosounders, while additional sensors positioned at different heights in the water column measured light, turbidity, chlorophyll, temperature, salinity, and water flow. Although this work is still ongoing, the aim is to relate sandeel presence in the water column to environmental drivers such as light conditions (including cloudy versus sunny weather), tidal dynamics, and other (a)biotic factors.



Figure 5: Left) Picture of the deployed WBAT frame. Right) The red dot indicates the location of the WBAT deployment on the sandeel distribution map from Chapter 2, including sandeel fishing grounds reported by Jensen et al. (2011).

6.3. Anthropogenic impacts

Sandeel fisheries have been suggested to reduce the availability of sandeel to other predator species in the UK (Daunt et al., 2008; Searle et al., 2023). In the Dutch coastal area, Tien et al. (2017) found that sandeel was negatively correlated with flatfish and shrimp fisheries. However a subsequent reanalysis indicated that this effect was weak (Zuur & Ieno, 2017). To my knowledge, the potential impact of sandeel fisheries themselves has not yet been studied in Dutch waters. Although sandeel fisheries in this area have historically been limited, this may change in the future. Fishers who previously operated in UK waters may seek alternative fishing grounds, including the Dutch EEZ, following the closure of sandeel fisheries there (ICES, 2026b). Therefore, the potential impact of increased sandeel fisheries in the Dutch EEZ warrants further attention.

Other anthropogenic activities may also impact small demersal fish including sandeel. No effect of sand suppletion was found on most demersal fish species, however, sandeel (both *Ammodytes* species as well as *H. lanceolatus*) appeared to be more aggregated in a specific area (van Hal et al., 2021). It remained unclear whether this pattern was directly caused by the supplementation or reflects natural interannual variation (van Hal et al., 2021). In contrast, sand extraction may have negative effects, as lower sandeel presence has been observed in newly dredged sandpits compared to surrounding areas, probably due to sediment silting (Witbaard et al., 2025). Future studies could examine the temporal dynamics of this effect, including the rate at which sandeel occurrence in the seabed recovers as silt content decreases. It is also important to assess whether these impacts extend to larger spatial scales and, if so, to determine the threshold at which dredging activity (e.g. the number of sandpits or the total surface area used for extraction) sandeel abundance is impacted. An additional question is whether similar effects occur for other small demersal fish species, and how other anthropogenic activities (offshore wind farms, fishing, oil and gas infrastructure, subsea cables, etc.) may influence the small demersal fish community.

It is important not only to improve understanding of how these activities affect small demersal fish and thereby alter prey availability for predators, but also to assess whether predator species themselves are impacted. For instance, sandeel appear to be only weakly affected by offshore wind farms (van Deurs et al., 2012), but as mentioned earlier, sandwich terns have been reported to avoid offshore wind farm areas (van Bemmelen et al., 2024). Overall, this highlights the need for a better understanding of anthropogenic impacts across both prey communities and higher trophic-level species.

7. MANAGEMENT IMPLICATIONS AND CONCLUDING REMARKS

The Dutch North Sea is a heavily human-influenced area, where activities include fisheries, resource extraction (such as sand, oil, and gas), maritime transport, and energy production by windfarms are abundant (Fig. 6). These human-induced pressures already affect the southern North Sea marine ecosystem (Emeis et al., 2015; Kenny et al., 2018; Watson et al., 2024), and are expected to increase further due to growing demand for energy (e.g. offshore wind) and natural resources (e.g. sand).

To reduce anthropogenic impacts on ecosystem health, the Netherlands has established targets in line with the EU requirement to achieve Good Environmental Status (GES) in its territorial waters (European Union, 2008; Ministry of Infrastructure and Water Management, 2022). GES targets include thresholds for population size, species distribution, and breeding success, particularly for higher trophic-level species such as seals, porpoise, seabirds, and commercial or large fish. To achieve species-specific GES targets, and thereby overall GES, measures to manage and mitigate the effects of human impacts may be required. An example of such a measure (outside the EU though) is the closure of sandeel fisheries in the UK, implemented to improve prey availability for predators and enhance marine ecosystem status (Appleby & Scott, 2026). Whether similar measures aimed at supporting predator populations through increased prey availability are necessary or effective in the Dutch EEZ remains largely unresolved, despite their clear ecological relevance. A thorough understanding of prey abundance and distribution for higher trophic-level predators is therefore required, as well as how this influences predator population dynamics, alongside a better understanding of how human activities interfere with prey–predator interactions.

In this thesis, we observed higher densities of small demersal fish than previously estimated, including the two most abundant sandeel species, using alternative sampling gear. The high abundances explain why small demersal fish constitute such a substantial part of the diet of seals and porpoise in the Dutch North Sea. Furthermore, the revised prey abundance estimates may change our understanding of how many predators can be supported, based on food availability, in the southern North Sea. The spatial analyses identified areas in the Dutch EEZ where small demersal fish abundance is particularly high (e.g. northwest of Texel). These areas may represent important foraging habitat for predator species, which is suggested by seal tracking data. The existence of such (unknown) hotspot areas may warrant additional consideration in spatial

planning, for example when designating protected areas or locating offshore wind farms and sand extraction activities, to minimise potential impacts from human activities.

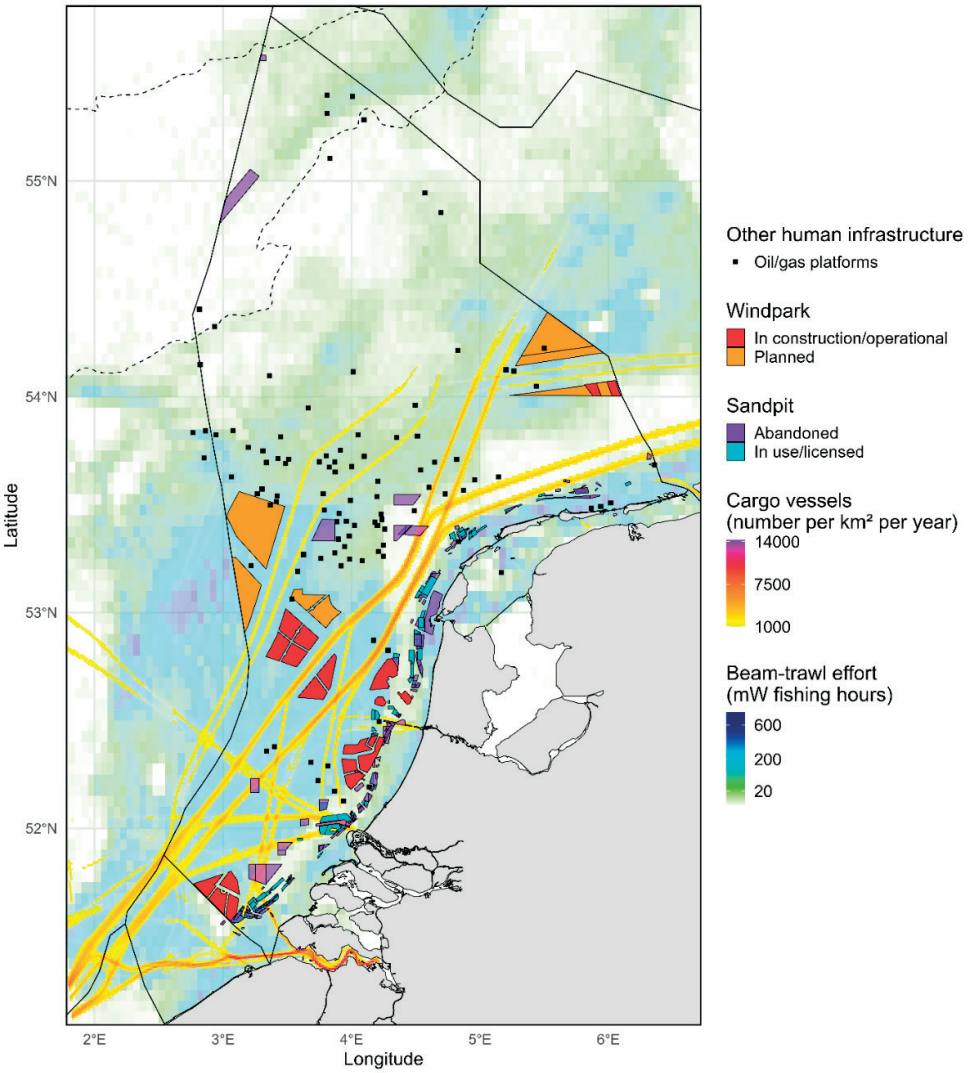


Figure 6: Human activities in the Dutch EEZ. Beam trawl effort (annual average, 2019–2022) also includes shrimp fisheries. Data for the different layers were obtained from Informatiehuis Marien and EMODnet. Other human infrastructures, such as cables and pipelines, are not included. Similarly, designated areas (e.g. for defence training, nature reserves, and fishing-restricted areas) are left out for clarity.

To conclude, this thesis demonstrates that the small demersal fish community can be quantified using alternative fish sampling methods. As a result, our understanding of multiple aspects of prey availability for small demersal fish and their importance to larger predator species has improved. Furthermore, the thesis provides a basis for future studies on small demersal fish themselves, as well as more direct predator–prey links, which may ultimately lead to evidence-based decision-making. In this way, it may contribute to a future in which the (southern) North Sea, and marine systems in general, are recognised not only for shipping, energy production, or resource extraction, but also for the richness of life they support, from the smallest to the largest organisms.

Appendices

References
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REFERENCES

Aarts, G., Brasseur, S., Poos, J. J., Schop, J., Kirkwood, R., van Kooten, T., Mul, E., Reijnders, P., Rijnsdorp, A. D., & Tulp, I. (2019). Top-down pressure on a coastal ecosystem by harbor seals. *Ecosphere*, *10*(1), e02538. https://doi.org/10.1002/ecs2.2538

Aarts, G., Cremer, J., Kirkwood, R., van der Wal, J. T., Matthiopoulos, J., & Brasseur, S. (2016). Spatial distribution and habitat preference of harbour seals (Phoca vitulina) in the Dutch North Sea. *Wageningen University & Research Report*, *C118/16*. https://doi.org/10.18174/400306

Albo-Puigserver, M., Sanchez, S., Coll, M., Bernal, M., Saez-Liante, R., Navarro, J., & Palomera, I. (2020). Year-round energy dynamics of sardine and anchovy in the northwestern Mediterranean Sea. *Marine Environmental Research*, *159*, 105021. https://doi.org/10.1016/j.marenvres.2020.105021

Anderson, H. B., Evans, P. G. H., Potts, J. M., Harris, M. P., & Wanless, S. (2014). The diet of common guillemot Uria aalge chicks provides evidence of changing prey communities in the North Sea. *Ibis*, *156*, 23–34. https://doi.org/10.1111/ibi.12099

Anderson, S. C., Ward, E. J., & Thorson, J. T. (2025). sdmTMB: An R Package for Fast, Flexible, and User-Friendly Generalized Linear Mixed Effects Models with Spatial and Spatiotemporal Random Fields. *Journal of Statistical Software*, *115*(2), 1–46. https://doi.org/10.18637/jss.v115.i02

Appleby, T., & Scott, J. (2026). Fisheries Versus the Environment Under Cover of a Trade. *International Journal for the Semiotics of Law*. https://doi.org/10.1007/s11196-026-10434-9

Atkins, J. R.C., Scaife, A. A., Graham, J. A., Tinker, J., & Halloran, P. R. (2025). Recent European marine heatwaves are unprecedented but not unexpected. *Communications Earth and Environment*, *6*(792). https://doi.org/10.1038/s43247-025-02802-3

Baker, M. R., Smeltz, T. S., Williams, K., Greufe, C., Ewing, M., Chapman, J., Glassy, J., Hasegawa, E., Cieri, K. P., Matson, S., & Towler, R. (2023). Diel vertical migration in Pacific sand lance (*Ammodytes personatus*)—A pelagic forage fish associated with benthic substrates. *ICES Journal of Marine Science*, 80(6), 1758–1772. https://doi.org/10.1093/icesjms/fsad106 '

Baldwin, C. C., Mounts, J. H., Smith, D. G., & Weigt, L. E. E. A. (2009). Genetic identification and color descriptions of early life-history stages of Belizean Phaeoptyx and Astrapogon (Teleostei: Apogonidae) with comments on identification of adult Phaeoptyx. *Zootaxa*, 1–22. https://doi.org/10.5281/zenodo.185742

Baptist, M. J., & Leopold, M. F. (2010). Prey capture success of sandwich terns sterna sandvicensis varies non-linearly with water transparency. *Ibis*, *152*(4), 815–825. https://doi.org/10.1111/j.1474-919X.2010.01054.x

Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Marshall, T. C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, *20*, 1023–1031. https://doi.org/10.1111/gcb.12514

Becker, S., Hanner, R., & Steinke, D. (2011). Five years of FISH-BOL: Brief status report. *Mitochondrial DNA*, *22*(sup1), 3–9. https://doi.org/10.3109/19401736.2010.535528

Bedford, M., Melbourne-Thomas, J., Corney, S., Jarvis, T., Kelly, N., & Constable, A. (2015). Prey-field use by a Southern Ocean top predator: Enhanced understanding using integrated datasets. *Marine Ecology Progress Series*, *526*, 169–181. https://doi.org/10.3354/meps11203

Behrens, J. W., Stahl, H. J., Steffensen, J. F., & Glud, R. N. (2007). Oxygen dynamics around buried lesser sandeels *Ammodytes* tobianus (Linnaeus 1785): mode of ventilation and oxygen requirements. *Journal of Experimental Biology*, *210*, 1006–1014. https://doi.org/10.1242/jeb.000570

Behrens, J. W., & Steffensen, J. F. (2007). The effect of hypoxia on behavioural and physiological aspects of lesser sandeel, *Ammodytes* tobianus (Linnaeus, 1785). *Marine Biology*, *150*(6), 1365–1377. https://doi.org/10.1007/s00227-006-0456-4

Benaksas, S., Lynam, C., Daunt, F., Nnanatu, C., Kooij, J. Van Der, & Webb, T. J. (n.d.). *Seabird prey in space and time: Combining multiple datasets to model the distribution of sandeel (Ammodytes marinus) and sprat (Sprattus sprattus) in the North Sea*. 1–47.

Benoit-Bird, K. J., Battaile, B. C., Heppell, S. A., Hoover, B., Irons, D., Jones, N., Kuletz, K. J., Nordstrom, C. A., Paredes, R., Suryan, R. M., Waluk, C. M., & Trites, A. W. (2013). Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLoS ONE*, *8*(1), e53348. https://doi.org/10.1371/journal.pone.0053348

Bergman, M. J. N., & van Santbrink, J. W. (1994). A new benthos dredge ('triple-D') for quantitative sampling of infauna species of low abundance. *Netherlands Journal of Sea Research*, *33*(1), 129–133. https://doi.org/10.1016/0077-7579(94)90057-4

Bergstad, O. A. (2009). Fish: Demersal fish (life histories, behavior, adaptations). *Encyclopedia of Ocean Sciences (Second Edition)*, 458–466. https://doi.org/10.1016/B978-012374473-9.00673-1

Bergstad, O. A., Hoines, Å. S., & Krüger-Johnsen, E. M. (2001). Spawning time, age and size at maturity, and fecundity of sandeel, *Ammodytes* marinus, in the north-eastern North Sea and in unfished coastal waters off Norway. *Aquatic Living Resources*, *14*(5), 293–301. https://doi.org/10.1016/S0990-7440(01)01134-2

Birt, V. L., Birt, T. P., Goulet, D., Cairnse, D. K., & Montevecchi, W. A. (1987). Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series*, 40, 205–208. https://doi.org/10.3354/meps040205

Bockelmann, F. D., Puls, W., Kleeberg, U., Müller, D., & Emeis, K. C. (2018). Mapping mud content and median grain-size of North Sea sediments – A geostatistical approach. *Marine Geology*, *397*, 60–71. https://doi.org/10.1016/j.margeo.2017.11.003

Bolle, L. J., Dapper, R., Witte, J. I. J., & van der Veer, H. W. (1994). Nursery grounds of dab (Limanda limanda L.) in the southern North Sea. *Netherlands Journal of Sea Research*, *32*(3–4), 299–307. https://doi.org/10.1016/0077-7579(94)90007-8

Booth, C. G., Guilpin, M., Darias-O'Hara, A., Ransijn, J. M., Ryder, M., Rosen, D., Pirotta, E., Costa, D. P., Smout, S., McHuron, E. A., & Nabe-Nielsen, J. (2023). Estimating energetic intake for marine mammal bioenergetic models. *Conservation Physiology*, *11*(1), coac083. https://doi.org/10.1093/conphys/coac083

Bossart, G. D. (2011). *Marine Mammals as Sentinel Species for Oceans and Human Health*. *48*(3), 676–690. https://doi.org/10.1177/0300985810388525

Brown, J. H., Gillooly, J. F., Allen, A. P., van Savage, M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789.

Burchard, H., & Bolding, K. (2002). GETM – a general estuarine transport model, Scientific documentation. *European Commission Technical Report*, EUR20253.

Bulman, C., Althaus, F., He, X., Bax, N. J., & Williams, A. (2001). Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. *Marine and Freshwater Research,* 52(4), 537–548. https://doi.org/10.1071/MF99152'

Callaway, R., Alsvåg, J., De Boois, I., Cotter, J., Ford, A., Hinz, H., Jennings, S., Kröncke, I., Lancaster, J., Piet, G., Prince, P., & Ehrich, S. (2002). Diversity and community structure of epibenthic invertebrates and fish in the North Sea. *ICES Journal of Marine Science*, *59*(6), 1199–1214. https://doi.org/10.1006/jmsc.2002.1288

Camphuysen, C. J. (2005). Understanding marine food web processes: An ecosystem approach to sustainable sandeel fisheries in the North Sea. In *IMPRESS Final Report*. http://www.vliz.be/imisdocs/publications/43/269143.pdf

Carlson, N. V, White, M. A. V, Tavera, J., Hara, P. D. O., Baker, M. R., Bertram, D. F., Summers, A., Fifield, D. A., Juanes, F., Valle, U., & Mel, C. U. (2025). Noise results in lower quality of an important forage fish, the Pacific sand lance, *Ammodytes* personatus. *Marine Pollution Bulletin*, *213*, 117664. https://doi.org/10.1016/j.marpolbul.2025.117664

Carroll, M. J., Bolton, M., Owen, E., Anderson, G. Q. A., Mackley, E. K., Dunn, E. K., & Furness, R. W. (2017). Kittiwake breeding success in the southern North Sea correlates with prior sandeel fishing mortality. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*(6), 1164–1175. https://doi.org/10.1002/aqc.2780

Carter, M. I. D., Aarts, G., Beest, F. M. Van, Bivins, M., Brasseur, S. M. J. M., Dietz, R., Duck, C. D., Galatius, A., Gilles, A., Haelters, J., Hastie, G. D., Jessopp, M., Morris, C. D., Moss, S. E. W., Nachtsheim, D. A., Schaffeld, T., Schop, J., Siebert, U., Teilmann, J., Thompson, D., Thompson, P. M., Vincent, C., & Russell, D. J. F. (2025). At sea distribution of seals on the Northwest European Shelf: Towards transboundary conservation and management. *Journal of Applied Ecology*, *63*(e70236). https://doi.org/10.1111/1365-2664.70236

Cheng, C. H., Soetaert, K., & Borsje, B. W. (2020). Sediment characteristics over asymmetrical tidal sand waves in the Dutch North Sea. *Journal of Marine Science and Engineering*, 8(6), 409. https://doi.org/10.3390/jmse8060409

CLO. 2023. Zeevissen, 1990–2021.www.clo.nl (November 2024, date last accessed).

Chen, W., Bonillo, C., & Lecointre, G. (2003). Repeatability of clades as a criterion of reliability: a case study for molecular phylogeny of Acanthomorpha (Teleostei) with larger number of taxa. *Molecular Phylogenetics and Evolution*, *26*(2), 262–288. https://doi.org/10.1016/S1055-7903(02)00371-8

Christensen, A., Butenschön, M., Gürkan, Z., & Allen, I. (2013). Towards an integrated forecasting system for fisheries on habitat-bound stocks. *Ocean Science*, *9*, 261–279. https://doi.org/10.5194/os-9-261-2013

Christensen, A., Jensen, H., Mosegaard, H., St. John, M., & Schrum, C. (2008). Sandeel (*Ammodytes* marinus) larval transport patterns in the North Sea from an individual-based hydrodynamic egg and larval model. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(7), 1498–1511. https://doi.org/10.1139/F08-073

Chudzinska, M., Nabe-Nielsen, J., Smout, S., Aarts, G., Brasseur, S., Graham, I., Thompson, P., & McConnell, B. (2021). AgentSeal: Agent-based model describing movement of marine central-place foragers. *Ecological Modelling*, *440*(November 2020), 109397. https://doi.org/10.1016/j.ecolmodel.2020.109397

Costa, F. O., Landi, M., Martins, R., Costa, M. H., Costa, M. E., Carneiro, M., Alves, M. J., Steinke, D., & Carvalho, G. R. (2012). A ranking system for reference libraries of DNA barcodes: application to marine fish species from Portugal. *PLoS ONE*, *7*(4), e35858. https://doi.org/10.1371/journal.pone.0035858

Costello, M. J., Basher, Z., Sayre, R., Breyer, S., & Wright, D. J. (2018). Stratifying ocean sampling globally and with depth to account for environmental variability. *Scientific Reports*, 8(11259). https://doi.org/10.1038/s41598-018-29419-1

Courtens, W., Verstraete, H., Vanermen, N., van de Walle, M., & Stienen, E. W. M. (2017). Faecal samples reveal the diet of breeding adult Sandwich terns Thalasseus sandvicensis in Belgium and the southern part of the Netherlands. *Journal of Sea Research*, *127*, 182–193. https://doi.org/10.1016/j.seares.2017.03.014

Cresci, A., Perrichon, P., Durif, C. M. F., Sørhus, E., Johnsen, E., Bjelland, R., Larsen, T., Skiftesvik, A. B., & Browman, H. I. (2022). Magnetic fields generated by the DC cables of offshore wind farms have no effect on spatial distribution or swimming behavior of lesser sandeel larvae (Ammodytes marinus). *Marine Environmental Research*, *176*, 105609. https://doi.org/10.1016/j.marenvres.2022.105609

Creutzberg, F., Wapenaar, P., Duineveld, G., & Lopez Lopez, N. (1984). Distribution and density of the benthic fauna in the southern North Sea in relation to bottom characteristics and hydrographic conditions. *Rapports et Procès-Verbaux Des Réunions Conseil Permanent International Pour l'exploration de La Mer*, *183*, 101–110.

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quiñones, R. A., Shannon, L. J., & Verheye, H. M. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science*, *57*(3), 603–618. https://doi.org/10.1006/jmsc.2000.0712

Cury, P. M., Boyd, I., Bonhommeua, S., Anker-Nilssen, T., Crawford, R. J. M., & Furness, R. W. (2011). Global seabird response to forage fish depletion—one-third for the birds. *Science, 334*(6063), 1703–1706. https://doi.org/10.1126/science.1212928

Daan, N., Gislason, H., Pope, J. G., & Rice, J. C. (2005). Changes in the North Sea fish community: Evidence of indirect effects of fishing? *ICES Journal of Marine Science*, *62*(2), 177–188. https://doi.org/10.1016/j.icesjms.2004.08.020

Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(31), 12788–12793. https://doi.org/10.1073/pnas.0902080106

Daunt, F., Wanless, S., Greenstreet, S. P. R., Jensen, H., Hamer, K. C., & Harris, M. P. (2008). The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(3), 362–381. https://doi.org/10.1139/F07-164

Doorenspleet, K., Jansen, L., Oosterbroek, S., Kamermans, P., Bos, O., & Wurz, E. (2025). The long and the short of it: Nanopore-based eDNA metabarcoding of marine vertebrates works; sensitivity and species-level assignment depend on amplicon lengths. *Molecular Ecology Resources*, 25, e14079. https://doi.org/10.1111/1755-0998.14079.

Malik, M. D. Al, Aulya, M., & Cahyani, N. K. D. (2026). DBP metabarcoding pipeline: An integrated tool for eDNA analysis of ONT data using the Indonesian marine fish database. *Regional Studies in Marine Science*, 95, 104868. https://doi.org/10.1016/j.rsma.2026.104868

Dubreuil, J., & Petitgas, P. (2009). Energy density of anchovy Engraulis encrasicolus in the Bay of Biscay. *Journal of Fish Biology*, *74*(3), 521–534. https://doi.org/10.1111/j.1095-8649.2008.02143.x

de Fouw, J., van Horssen, P. W., Craeymeersch, J., Leopold, M. F., Perdon, J., Troost, K., Tulp, I., van Zwol, J., & Philippart, C. J. M. (2024). Spatio-temporal analysis of potential factors explaining fluctuations in population size of *Spisula subtruncata* in the Dutch North Sea. *Frontiers in Marine Science*, 11(1476223). https://doi.org/10.3389/fmars.2024.1476223

Devroye, L. (1986). Non-uniform random variate generation. Springer.

Duineveld, G. C. A., Konitzer, A., Niermann, U., de Wilde, P. A. W. J., & Gray, J. S. (1991). The macrobenthos of the North Sea. *Journal of Sea Research*, *28*, 53–65.

Emeis, K., van Beusekom, J., Callies, U., Ebinghaus, R., Kannen, A., Kraus, G., Kröncke, I., Lenhart, H., Lorkowski, I., Matthias, V., Möllmann, C., Pätsch, J., Scharfe, M., Thomas, H., Weisse, R., & Zorita, E. (2015). The North Sea — A shelf sea in the Anthropocene. *Journal of Marine Systems*, *141*, 18–33. https://doi.org/10.1016/j.jmarsys.2014.03.012

Engelhard, G. H., Blanchard, J. L., Pinnegar, J. K., van der Kooij, J., Bell, E. D., Mackinson, S., & Righton, D. A. (2013). Body condition of predatory fishes linked to the availability of sandeels. *Marine Biology*, *160*(2), 299–308. https://doi.org/10.1007/s00227-012-2088-1

Engelhard, G. H., Ellis, J. R., Payne, M. R., ter Hofstede, R., & Pinnegar, J. K. (2011). Ecotypes as a concept for exploring responses to climate change in fish assemblages. *ICES Journal of Marine Science*, *68*(3), 580–591. https://doi.org/10.1093/icesjms/fsq183

Engelhard, G. H., Peck, M. A., Rindorf, A., Smout, S. C., van Deurs, M., Raab, K., Andersen, K. H., Garthe, S., Lauerburg, R. A. M., Scott, F., Brunel, T., Aarts, G., van Kooten, T., & Dickey-Collas, M. (2014). Forage fish, their fisheries, and their predators: who drives whom? *ICES Journal of Marine Science*, *71*(1), 90–104. https://doi.org/10.1093/icesjms/fst087

Engelhard, G. H., van der Kooij, J., Bell, E. D., Pinnegar, J. K., Blanchard, J. L., Mackinson, S., & Righton, D. A. (2008). Fishing mortality versus natural predation on diurnally migrating sandeels Ammodytes marinus. *Marine Ecology Progress Series*, *369*, 213–227. https://doi.org/10.3354/meps07575

European Union. (2008). Directive 2008/56/EC of the European Parliament and of the Council. *Official Journal of the European Union*, 19–40.

Fauchald, P. (2009). Spatial interaction between seabirds and prey: Review and synthesis. *Marine Ecology Progress Series*, *391*, 139–151. https://doi.org/10.3354/meps07818

Fijn, R. C., Courtens, W., Engels, B. W. R., Loon, E. E. Van, & Shamoun-baranes, J. (2024). Combining video and GPS-tracking to study the spatial foraging distribution of a single-prey loading seabird. *Avian Research*, *15*(October 2023), 100196. https://doi.org/10.1016/j.avrs.2024.100196

Fijn, R. C., de Jong, J., Courtens, W., Verstraete, H., Stienen, E. W. M., & Poot, M. J. M. (2017). GPS-tracking and colony observations reveal variation in offshore habitat use and foraging ecology of breeding Sandwich Terns. *Journal of Sea Research*, *127*, 203–211. https://doi.org/10.1016/j.seares.2016.11.005

Fijn, R. C., Thaxter, C. B., Aarts, G., Adema, J., Middelveld, R. P., & van Bemmelen, R. S. A. (2022). Relative effects of static and dynamic abiotic conditions on foraging behaviour in breeding Sandwich terns. *Marine Ecology Progress Series*, *692*, 137–150. https://doi.org/10.3354/meps14076

Flores-Ortega, J. R., Godinez-Dominiguez, E., & Gonzales-Sanson, G. (2020). Trophic interactions between the 11 most abundant demersal fish species on the Pacific coast of central Mexico. *Ciencias Marinas*, 46(2), 101–117. https://doi.org/10.7773/cm.v46i2.3056

Fonds, M. (1973). Sand gobies in the Dutch Wadden Sea (pomatoschistus, gobiidae, pisces). *Netherlands Journal of Sea Research*, *6*(4), 417–478. https://doi.org/10.1016/0077-7579(73)90001-X

Fraser, H. M., Greenstreet, S. P. R., & Piet, G. J. (2007). Taking account of catchability in groundfish survey trawls: Implications for estimating demersal fish biomass. *ICES Journal of Marine Science*, *64*(9), 1800–1819. https://doi.org/10.1093/icesjms/fsm145

Frederiksen, M., Furness, R. W., & Wanless, S. (2007). Regional variation in the role of bottom-up and top-down processes in controlling sandeel abundance in the North Sea. *Marine Ecology Progress Series*, *337*, 279–286. https://doi.org/10.3354/meps337279

Free, C. M., Jensen, O. P., & Hilborn, R. (2021). Evaluating impacts of forage fish abundance on marine predators. *Conservation Biology*, *35*(5), 1540–1551. https://doi.org/10.1111/cobi.13709

Freeman, S., MacKinson, S., & Flatt, R. (2004). Diel patterns in the habitat utilisation of sandeels revealed using integrated acoustic surveys. *Journal of Experimental Marine Biology and Ecology*, *305*(2), 141–154. https://doi.org/10.1016/j.jembe.2003.12.016

Friedlaender, A. S., Hazen, E. L., Nowacek, D. P., Halpin, P. N., Ware, C., Weinrich, M. T., Hurst, T., & Wiley, D. (2009). Diel changes in humpback whale *Megaptera novaeangliae* feeding behavior in response to sand lance Ammodytes spp. behavior and distribution. *Marine Ecology Progress Series*, 395, 91–100. https://doi.org/10.3354/meps08003

Froese, R., & Pauly, D. (2026). *FishBase*. www.fishbase.org

Furness, R. W. (1990). A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981–83. *Ibis*, *132*(2), 205–217. https://doi.org/10.1111/j.1474-919X.1990.tb01039.x

Furness, Robert W. (2002). Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *ICES Journal of Marine Science*, *59*(2), 261–269. https://doi.org/10.1006/jmsc.2001.1155

Galatius, A., Brasseur, S., Hamm, T., Armin, J., Meise, K., Meyer, J., Schop, J., Siebert, U., Stejskal, O., Teilmann, J., & Thøstesen, C. B. (2025). Survey results of harbour seals in the Wadden Sea. *Common Wadden Sea Secretariat*.

Gibson, R. N., Robb, L., Wennhage, H., & Burrows, M. T. (2002). *Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground*. *229*, 233–244.

Gilles, A., Viquerat, S., Becker, E. A., Forney, K. A., Geelhoed, S. C. V., Haelters, J., Nabe-Nielsen, J., Scheidat, M., Siebert, U., Sveegaard, S., van Beest, F. M., van Bemmelen, R., & Aarts, G. (2016). Seasonal habitat-based density models for a marine top predator, the harbor porpoise, in a dynamic environment. *Ecosphere*, *7*(6), 1–22. https://doi.org/10.1002/ecs2.1367

Gladyshev, M. I., Suschik, N. N., Tolomeev, A. P., & Dgebuadze, Y. Y. (2018). Meta-analysis of factors associated with omega-3 fatty acid contents of wild fish. *Reviews in Fish Biology and Fisheries*, *28*(2), 277–299. https://doi.org/10.1007/s11160-017-9511-0

Green, D. B., Bestley, S., Trebilco, R., Corney, S. P., Lehodey, P., McMahon, C. R., Guinet, C., & Hindell, M. A. (2020). Modelled mid-trophic pelagic prey fields improve understanding of marine predator foraging behaviour. *Ecography*, *43*, 1014–1026. https://doi.org/10.1111/ecog.04939

Greenstreet, S. P. R., McMillan, J. A., & Armstrong, E. (1998). Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: A response to variation in prey abundance? *ICES Journal of Marine Science*, 55(1), 121–133. https://doi.org/10.1006/jmsc.1997.0258

Greenstreet, S. P. R., Armstrong, E., Mosegaard, H., Jensen, H., Gibb, I. M., Fraser, H. M., Scott, B. E., Holland, G. J., & Sharples, J. (2006). Variation in the abundance of sandeels Ammodytes marinus off southeast Scotland: an evaluation of area-closure fisheries management and stock abundance assessment methods. *ICES Journal of Marine Science*, *63*(8), 1530–1550. https://doi.org/10.1016/j.icesjms.2006.05.009

Greenstreet, S., Fraser, H., Piet, G., Robinson, L., Callaway, R., Reiss, H., Ehrich, S., Kröncke, I., Craeymeersch, J., Lancaster, J., Jorgensen, L., & Goffin, A. (2007). Species Composition, Diversity, Biomass and Production of the Demersal Fish Community of the North Sea. *Fisheries Research Services Collaborative Report*, *07/07*.

Haelters, J., Kerckhof, F., Jacques, T. G., & Degraer, S. (2011). The harbour porpoise Phocoena phocoena in the Belgian part of the North Sea: Trends in abundance and distribution. *Belgian Journal of Zoology*, *141*(2), 75–84.

Han, Z., Yanagimoto, T., Zhang, Y., & Gao, T. (2012). Phylogeography study of Ammodytes personatus in Northwestern Pacific: Pleistocene isolation, temperature and current conducted secondary contact. *PLoS ONE*, *7*(5), e37425. https://doi.org/10.1371/journal.pone.0037425

Härkönen, T., & Heide-Jørgensen, M. (1991). The harbour seal Phoca vitulina as a predator in the Skagerrak. *Ophelia*, *34*(3), 191–207. https://doi.org/10.1080/00785326.1991.10429695

Heessen, H. J. L., Daan, N., & Ellis, J. R. (2015). *Fish atlas of the Celtic Sea, North Sea, and Baltic Sea: Based on international research-vessel surveys*. Wageningen Academic Publishers.

Henriksen, O., Moran, N. P., Veilex, L. A., Behrens, J. W., Nielsen, A., Mildenberger, T. K., Wright, P. J., Jensen, H., & van Deurs, M. (2024). Effects of sediment type and light availability on the burying behaviour of small sandeel (Ammodytes tobianus). *Journal of Experimental Marine Biology and Ecology*, *577*(152020). https://doi.org/10.1016/j.jembe.2024.152020

Henriksen, O., Rindorf, A., Mosegaard, H., Payne, M. R., & van Deurs, M. (2021). Get up early: Revealing behavioral responses of sandeel to ocean warming using commercial catch data. *Ecology and Evolution*, *11*, 16786–16805. https://doi.org/10.1002/ece3.8310

Heße, E., Boyi, J. O., Das, K., Lehnert, K., Piette, M., Pinzone, M., Siebert, U., & Gilles, A. (2026). Rising competition among North Sea mammalian top predators : a multi-method perspective on trophic ecology. *Scientific Reports*, *16*(15172). https://doi.org/https://doi.org/10.1038/s41598-026-53094-2 1

Hiddink, J. G., & ter Hofstede, R. (2008). Climate induced increases in species richness of marine fishes. *Global Change Biology*, *14*(3), 453–460. https://doi.org/10.1111/j.1365-2486.2007.01518.x

Hislop, J. R. G., Harris, M. P., & Smith, J. G. M. (1991). Variation in the calorific value and total energy content of the lesser sandeel (Ammodytes marinus) and other fish preyed on by seabirds. *Journal of Zoology*, *224*(3), 501–517. https://doi.org/10.1111/j.1469-7998.1991.tb06039.x

Holland, G. J., Greenstreet, S. P. R., Gibb, I. M., Fraser, H. M., & Robertson, M. R. (2005). Identifying sandeel Ammodytes marinus sediment habitat preferences in the marine environment. *Marine Ecology Progress Series*, *303*, 269–282. https://doi.org/10.3354/meps303269

Holt, J., & Umlauf, L. (2008). Modelling the tidal mixing fronts and seasonal stratification of the Northwest European Continental shelf. *Continental Shelf Research*, *28*(7), 887–903. https://doi.org/10.1016/j.csr.2008.01.012

Howells, R. J., Burthe, S. J., Green, J. A., Harris, M. P., Newell, M. A., Butler, A., Wanless, S., & Daunt, F. (2019). Pronounced long-term trends in year-round diet composition of the European shag Phalacrocorax aristotelis. *Marine Biology*, *165*(12), 1–15. https://doi.org/10.1007/s00227-018-3433-9

Hunt, G. L., Engelhard, G. H., Wigham, B. D., & Pinnegar, J. K. (2025). Scale changes in the feeding patterns of demersal fish species in the western North Sea. *Fish and Fisheries*, *27*, 99–115. https://doi.org/10.1111/faf.70035

Hunter, E., Metcalfe, J. D., & Reynolds, J. D. (2003). Migration route and spawning area fidelity by North Sea plaice. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1529), 2097–2103. https://doi.org/10.1098/rspb.2003.2473

ICES. (2004). Report of the Working Group on Fish Ecology, Relative catchabilities of common fish species in different survey gears. *ICES CM*, *G:09*.

ICES. (2022). International Bottom Trawl Survey Working Group (IBTSWG). *ICES Scientific Reports*, *04*(65). https://doi.org/10.17895/ices.pub.20502828

ICES. (2023a). Benchmark workshop on sandeel (Ammodytes spp.) (Outputs from 2022 and 2023 meetings) (WKSANDEEL). *ICES Scientific Reports*, *6*(10). https://doi.org/10.17895/ices.pub.21581151

ICES. (2023b). Dab (Limanda limanda) in Subarea 4 and Division 3.a (North Sea, Skagerrak and Kattegat). *ICES Advice*. https://doi.org/10.17895/ices.advice.22793633

ICES. (2023c). Plaice (Pleuronectes platessa) in Subarea 4 (North Sea) and Subdivision 20 (Skagerrak). Replacing advice provided in 2022. *ICES Advice*, *4*(April), 1–12. https://doi.org/10.17895/ices.advice.22548568

ICES. (2024a). Herring Assessment Working Group (HAWG). *ICES Scientific Reports*, *06*(24). https://doi.org/10.17895/ices.pub.25305532

ICES. (2024b). ICES Survey Protocols – Inshore beam trawl surveys, coordinated by Working Group on Beam Trawl Surveys (WGBEAM). *ICES Techniques in Marine Environmental Studies*, *70*. https://doi.org/10.17895/ices.pub.25382437

ICES. (2024c). 6.3.40 Sandeel (Ammodytes spp.) in Divisions 4a and 4b, Sandeel Area 4 (North and Central North Sea). *ICES Advice*, *4*, 1–6. https://doi.org/https://doi.org/10.17895/ices.advice.25019657

ICES. (2025a). Greater North Sea ecoregion – fisheries overview. *ICES Advice*. https://doi.org/10.17895/ices.advice.30710897

ICES. (2025b). Sandeel (Ammodytes spp.) in divisions 4.b–c, Sandeel Area 1r (central and southern North Sea, Dogger Bank). *ICES Advice*. https://doi.org/10.17895/ices.advice.27202845

ICES. (2026a). *Sandeel (Ammodytes spp.) in divisions 4.b–c and Subdivision 20, sandeel Area 2r (central and southern North Sea)*. *February 2026*, 1–7.

ICES. (2026b). Sandeel (Ammodytes spp .) in divisions 4 . b – c , Sandeel Area 1r (central and southern North Sea, Dogger Bank). *ICES Advice*. https://doi.org/10.17895/ices.advice.31430305

IJsseldijk, L. L., Hessing, S., Mairo, A., ten Doeschate, M. T. I., Treep, J., van den Broek, J., Keijl, G. O., Siebert, U., Heesterbeek, H., Gröne, A., & Leopold, M. F. (2021). Nutritional status and prey energy density govern reproductive success in a small cetacean. *Scientific Reports*, *11*(1), 1–13. https://doi.org/10.1038/s41598-021-98629-x

Jansen, O. E., Michel, L., Lepoint, G., Das, K., Couperus, A. S., & Reijnders, P. J. H. (2013). Diet of harbor porpoises along the Dutch coast: A combined stable isotope and stomach contents approach. *Marine Mammal Science*, *29*(3), 295–311. https://doi.org/10.1111/j.1748-7692.2012.00621.x

Jennings, S., & Blanchard, J. L. (2004). *Fish abundance with no fishing: predictions based on macroecological theory*. *73*, 632–642. https://doi.org/10.1111/j.0021-8790.2004.00839.x

Jensen, H., Rindorf, A., Wright, P. J., & Mosegaard, H. (2011). Inferring the location and scale of mixing between habitat areas of lesser sandeel through information from the fishery. *ICES Journal of Marine Science*, *68*(1), 43–51. https://doi.org/10.1093/icesjms/fsq154

Johnsen, E., & Harbitz, A. (2013). Small-scale spatial structuring of burrowed sandeels and the catching properties of the dredge. *ICES Journal of Marine Science*, *70*, 379–386. https://doi.org/icesjms/fss202

Johnson, B. M., Pate, W. M., & Hansen, A. G. (2017). Energy density and dry matter content in fish: New observations and an evaluation of some empirical models. *Transactions of the American Fisheries Society*, *146*, 1262–1278. https://doi.org/10.1080/00028487.2017.1360392

Jones, D. I., Miethe, T., Clarke, E. D., & Marshall, C. T. (2023). Disentangling the effects of fishing and temperature to explain increasing fish species richness in the North Sea. *Biodiversity and Conservation*, *32*(10), 3133–3155. https://doi.org/10.1007/s10531-023-02643-6

Jørgensen, M. G. P., van Deurs, M., Anthony, I., Butts, E., Jørgensen, K., & Behrens, J. W. (2017). PIT-tagging method for small fishes: A case study using sandeel (Ammodytes tobianus). *Fisheries Research*, *193*(November 2016), 95–103. https://doi.org/10.1016/j.fishres.2017.04.002

Kappa, F., Härkönen, T., Freitas, C., & Carroll, D. (2026). Shifting harbor seal (Phoca vitulina) diet may reflect ecosystem changes in Skagerrak. *Marine Mammal Science*, *42*(1), 1–12. https://doi.org/10.1111/mms.70069

Kenny, A. J., Jenkins, C., Wood, D., Bolam, S. G., Mitchell, P., Scougal, C., & Judd, A. (2018). Assessing cumulative human activities, pressures, and impacts on North Sea benthic habitats using a biological traits approach. *ICES Journal of Marine Science*, *75*(3), 1080–1092. https://doi.org/10.1093/icesjms/fsx205

Knebelsberger, T., Landi, M., Neumann, H., Kloppmann, M., Sell, A. F., Campbell, P. D., Laakmann, S., Raupach, M. J., & Carvalho, G. R. (2014). A reliable DNA barcode reference library for the identification of the North European shelf fish fauna. *Molecular Ecology Resources*, *14*, 1060–1071. https://doi.org/10.1111/1755-0998.12238

Knijn, R., Boon, T., Heessen, H., & Hislop, J. (1993). Atlas of North Sea Fishes. *ICES Cooperative Research Report*, *194*.

Komiyama, S., Holmin, A. J., Pedersen, G., & Johnsen, E. (2024). Silent uncrewed surface vehicles reveal the diurnal vertical distribution of lesser sandeel. *ICES Journal of Marine Science*, *0*(0), 1–15. https://doi.org/10.1093/ICESJMS/FSAE159

Langton, R., Boulcott, P., & Wright, P. (2021). A verified distribution model for the lesser sandeel Ammodytes marinus. *Marine Ecology Progress Series*, *667*, 145–159. https://doi.org/10.3354/meps13693

Leopold, M. F. (2015). *Eat and be eaten: porpoise diet studies*. Wageningen University.

Leopold, M. F., van Damme, C. J. G., & van der Veer, H. W. (1998). Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea. *Journal of Sea Research*, *40*, 93–107. https://doi.org/10.1016/S1385-1101(98)00028-8

Lin, J., Liang, Y., Zhao, H., & Gutang, Q. (2023). Better or worse food: Nutrition value of the prey fishes and the potential health implications for Indo-Pacific humpback dolphins. *Frontiers in Marine Science*, *10*, 1144398. https://doi.org/10.3389/fmars.2023.1144398

Lindgren, F., Rue, H., & Lindström, J. (2011). An explicit link between Gaussian fields and Gaussian Markov random fields: The stochastic partial differential equation approach. *Journal of the Royal Statistical Society Series B: Statistical Methodology*, *73*(4), 423–498. https://doi.org/10.1111/j.1467-9868.2011.00777.x

Link, J. S., & Garrison, L. P. (2002). Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US continental shelf. *Marine Ecology Progress Series*, 227, 109–123. https://doi.org/10.3354/meps227109

Ludwig, K. E., Singer, A., Kröncke, I., & Sell, A. F. (2024). Predator–prey trait associations and feeding preferences of demersal fishes in the southern North Sea. *Marine Ecology Progress Series*, *739*, 173–190. https://doi.org/10.3354/meps14597

Ludwig, W., Strunk, O., Westram, R., Richter, L., Meier, H., Buchner, A., Lai, T., Steppi, S., Jobb, G., Fo, W., Brettske, I., Gerber, S., Ginhart, A. W., Gross, O., Grumann, S., Liss, T., Lu, R., Hermann, S., Jost, R., Ko, A., Nonhoff, È., Reichel, B., Strehlow, R., Stamatakis, A., May, M., Stuckmann, N., Vilbig, A., Lenke, M., Ludwig, T., & Bode, A. (2004). ARB: a software environment for sequence data. *Nucleic Acids Research*, *32*(4), 1363–1371. https://doi.org/10.1093/nar/gkh293

Lynam, C. P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G. A., & Stenseth, N. C. (2017). Interaction between top-down and bottom-up control in marine food webs. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(8), 1952–1957. https://doi.org/10.1073/pnas.1621037114

Lynam, C. P., & Piet, G. (2023). Proportion of large fish (Large Fish Index). In: *The 2023 Quality Status Report for the Northeast Atlantic*, OSPAR Commission, 2023. https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/proportion-lfi/ (November 2024, date last accessed).

Maathuis, M. A. M., Manche, P., Couperus, B., Parmentier, B., Poos, J. J., Poot, M., Schekkerman, H., Sakinan, S., & Tulp, I. (2025a). The small pelagic fish food landscape and its use by common terns Sterna hirundo in the Wadden Sea. *Marine Biology*, *172*(6). https://doi.org/10.1007/s00227-025-04640-5

Maathuis, M. A. M., Berg, F., Couperus, B., Poos, J. J., & Tulp, I. (2025b). The function of the Wadden Sea in the life cycle of small pelagic fish. *Estuarine, Coastal and Shelf Science*, *313*, 109043. https://doi.org/10.1016/j.ecss.2024.109043

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. T*he American Naturalist*, *100*(916), 603–609. https://doi.org/10.1086/282454'

Macdougall, D. A. I., & Robinson, K. P. (2025). Following the food: Dynamic, seasonal changes in the fine-scale distribution of foraging minke whales within a Scottish Marine Protected Area (MPA). *Oceans*, *6*(1), 18. https://doi.org/10.3390/oceans6010018

Macer, C. T. (1966). Sand eels (Ammodytidae) in the south-western North Sea; their biology and fishery. *Ministry of Agriculture, Fisheries and Food, Fisheries Investigations*, *24*(6).

Mackenzie, B. R., & Schiedek, D. (2007). Daily ocean monitoring since the 1860s shows record warming of northern European seas. *Global Change Biology*, 13(7), 1335–1347. https://doi.org/10.1111/j.1365-2486.2007.01360.x

Mackinson, S., Turner, K., Righton, D., & Metcalfe, J. D. (2005). Using acoustics to investigate changes in efficiency of a sandeel dredge. *Fisheries Research*, *71*(3), 357–363. https://doi.org/10.1016/j.fishres.2004.09.002

MacLeod, C. D., Santos, M. B., Reid, R. J., Scott, B. E., & Pierce, G. J. (2007). Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: Could climate change mean more starving porpoises? *Biology Letters*, *3*(2), 185–188. https://doi.org/10.1098/rsbl.2006.0588

Madden, H. M., van der Have, T. M., & Fijn, R. C. (2025). Foraging areas of coastal and offshore seabirds in the Dutch North Sea. An analysis of survey and tracking data. *Waardenburg Ecology*, *25–134*.

McConnell, B. J., Fedak, M. A., Lovell, P., & Hammond, P. S. (1999). Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology*, *36*, 573–590. https://doi.org/10.1046/j.1365-2664.1999.00429.x

Mcgarigal, K., Yi, H., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling : a review and outlook. *Landscape Ecology*, *31*(6), 1161–1175. https://doi.org/10.1007/s10980-016-0374-x

Ministry of Infrastructure and Water Management. (2022). *Marine Strategy for the Dutch section of the North Sea 2022-2027 (part 3)*.

Morita, M., Ohnishi, M., Arakawa, E., Bhuiyan, N. A., Nusrin, S., & Alam, M. (2008). Development and validation of a mismatch amplification mutation PCR assay to monitor the dissemination of an emerging variant of Vibrio cholerae O1 biotype El Tor. *Microbiology and Immunology*, *52*(6), 314–317. https://doi.org/10.1111/j.1348-0421.2008.00041.x

Nævdal, B. G., & Thorkildsen, S. (2002). Genetic studies on species composition and population structure of sand eels (Genera: Ammodytes, Hyperoplus and Gymnammodytes) in Norwegian waters. *Journal of Applied Ichthyology*, *18*, 124–126. https://doi.org/10.1046/j.1439-0426.2002.00310.x

Neumann, H., Reiss, H., Ehrich, S., Sell, A., Panten, K., Kloppmann, M., Wilhelms, I., & Kröncke, I. (2013). Benthos and demersal fish habitats in the German Exclusive Economic Zone (EEZ) of the North Sea. *Helgoland Marine Research*, *67*(3), 445–459. https://doi.org/10.1007/s10152-012-0334-z

O'Connell, M., & Fives, J. M. (1995). The biology of the lesser sand-eel Ammodytes tobianus L. in the Galway Bay area. *Biology and Environment: Proceedings of the Royal Irish Academy*, *95B*(2), 87–98.

Olsson, O., Brown, J. S., & Helf, K. L. (2008). *A guide to central place effects in foraging*. *74*, 22–33. https://doi.org/10.1016/j.tpb.2008.04.005

Osterblom, H., Olsson, O., Blenckner, T., & Furness, R. W. (2008). Junk-food in marine ecosystems. *Oikos*, *117*, 967–977. https://doi.org/10.1111/j.2008.0030-1299.16501.x

Ovegård, M., & Valentinsson, D. (2026). Estimating escapees using automated video analysis: Assessing the sorting efficiency of the Excluder in the North Sea sandeel fishery. *Fisheries Research*, *294*, 107666. https://doi.org/10.1016/j.fishres.2026.107666

Parmentier, B., Aarts, G., Brasseur, S., Engelhard, G. H., Immler, E., van Langevelde, F., Tulp, I., & Witbaard, R. (2025). Small fish biomass in the North Sea is far greater than previously estimated. *ICES Journal of Marine Science*, *82*(6), 1–13. https://doi.org/10.1093/icesjms/fsaf082

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S., & Reid, J. B. (2008). *Seabirds as indicators of the marine environment*. 1520–1526.

Pedersen, J., & Hislop, J. R. G. (2001). Seasonal variations in the energy density of fishes in the North Sea. *Journal of Fish Biology*, *59*(2), 380–389. https://doi.org/10.1006/jfbi.2001.1649

Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Sumaila, U. R., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Heppell, S. S., Houde, E. D., Mangel, M., Plagányi, É., Sainsbury, K., Steneck, R. S., Geers, T. M., Gownaris, N., & Munch, S. B. (2014). The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries*, *15*(1), 43–64. https://doi.org/10.1111/faf.12004

Prins, T. C., Desmit, X., & Baretta-Bekker, J. G. (2012). Phytoplankton composition in Dutch coastal waters responds to changes in riverine nutrient loads. *Journal of Sea Research*, *73*, 49–62. https://doi.org/10.1016/j.seares.2012.06.009

Randall, R. G., & Minns, C. K. (2000). Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*, 1657–1667. https://doi.org/10.1139/f00-103

Ransijn, J. M., Booth, C., & Smout, S. C. (2019). A calorific map of harbour porpoise prey in the North Sea. *JNCC Report*, *633*.

Reay, P. (1970). Synopsis of the biological data on North Atlantic sand eels of the genus Ammodytes. *FAO Fish Synopsis*, *82*(56), 945–950.

Régnier, T., Wright, P. J., Harris, M. P., Gibb, F. M., Newell, M., Eerkes-Medrano, D., Daunt, F., & Wanless, S. (2024). Effect of timing and abundance of lesser sandeel on the breeding success of a North Sea seabird community. *Marine Ecology Progress Series*, *727*, 1–17. https://doi.org/10.3354/meps14520

Reiss, H., Degraer, S., Duineveld, G. C. A., Kröncke, I., Aldridge, J., Craeymeersch, J. A., Eggleton, J. D., Hillewaert, H., Lavaleye, M. S. S., Moll, A., Pohlmann, T., Rachor, E., Robertson, M., Vanden Berghe, E., van Hoey, G., & Rees, H. L. (2010). Spatial patterns of infauna, epifauna, and demersal fish communities in the North Sea. *ICES Journal of Marine Science*, *67*(2), 278–293. https://doi.org/10.1093/icesjms/fsp253

Reiss, H., Kröncke, I., & Ehrich, S. (2006). Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. *ICES Journal of Marine Science*, *63*(8), 1453–1464. https://doi.org/10.1016/j.icesjms.2006.06.001

Riaz, J., Bestley, S., Wotherspoon, S., Cox, M. J., & Emmerson, L. (2023). Spatial link between Adélie penguin foraging effort and krill swarm abundance and distribution. *Frontiers in Marine Science*, *10*, 1060984. https://doi.org/10.3389/fmars.2023.1060984

Rijnsdorp, A. D. (1993). Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, Pleuronectes platessa L. *Oecologia*, *96*(3), 391–401. https://doi.org/10.1007/BF00317510

Rijnsdorp, Adriaan D., van Leeuwen, P. I., Daan, N., & Heessen, H. J. L. (1996). Changes in abundance of demersal fish species in the North Sea between 1906-1909 and 1990-1995. *ICES Journal of Marine Science*, *53*(6), 1054–1062. https://doi.org/10.1006/jmsc.1996.0132

Rindorf, A., Wanless, S., & Harris, M. P. (2000). Effects of changes in sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series*, *202*, 241–252. https://doi.org/10.3354/meps202241

Rogers, S. I., & Ellis, J. R. (2000). Changes in the demersal fish assemblages of British coastal waters during the 20th century. *ICES Journal of Marine Science*, *57*(4), 866–881. https://doi.org/10.1006/jmsc.2000.0574

Rudbeck, L., & Dissing, J. (1998). Rapid, simple alkaline extraction of human genomic DNA from whole blood, buccal epithelial cells, semen and forensic stains for PCR. *BioTechniques*, *25*(4), 588–592. https://doi.org/10.2144/98254bm09

Rue, H., Martino, S., & Chopin, N. (2009). Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *Journal of the Royal Statistical Society Series B: Statistical Methodology Series B: Statistical Methodology*, *71*(2), 319–392. https://doi.org/10.1111/j.1467-9868.2008.00700.x

Sawada, K., Watanabe, Y., Kobayashi, K., Magome, Y., Abe, H., & Kamijo, T. (2025). Multidimensional niche partitioning allows coexistence of multiple snake species. Journal of Zoology, 325(4), 323–333. https://doi.org/10.1111/jzo.13259

Scharnweber, K., & Gardmark, A. (2020). Feeding specialists on fatty acid-rich prey have higher gonad weights: Pay-off in Baltic perch? *Ecosphere*, *11*(8), e03234. https://doi.org/10.1002/ecs2.3234

Schneider von Deimling, J., Hoffmann, J., Geersen, J., Koschinski, S., Lohrberg, A., Gilles, A., Belkin, I., Böttner, C., Papenmeier, S., & Krastel, S. (2023). Millions of seafloor pits, not pockmarks, induced by vertebrates in the North Sea. *Communications Earth and Environment*, *4*(1), 1–10. https://doi.org/10.1038/s43247-023-01102-y

Schoener, T. W. (1974). Resource partitioning in ecological communities. Science, 185(4145), 27–39. https://doi.org/10.1126/science.185.4145.27

Schultz, J. T., Aarts, G., Baptist, M., & Poos, J. (2025). Unravelling the impact of sand extraction pits on macrobenthos distribution in the Southern North Sea. *Marine Ecology Progress Series*, *772*, 43–60. https://doi.org/10.3354/meps14965

Searle, K. R., Regan, C. E., Perrow, M. R., Butler, A., Rindorf, A., Harris, M. P., Newell, M. A., Wanless, S., & Daunt, F. (2023). Effects of a fishery closure and prey abundance on seabird diet and breeding success: Implications for strategic fisheries management and seabird conservation. *Biological Conservation*, *281*, 109990. https://doi.org/10.1016/j.biocon.2023.109990

Sell, A. F., & Kröncke, I. (2013). Correlations between benthic habitats and demersal fish assemblages - A case study on the Dogger Bank (North Sea). *Journal of Sea Research*, *80*, 12–24. https://doi.org/10.1016/j.seares.2013.01.007

Sharples, R. J., Arrizabalaga, B., & Hammond, P. S. (2009). Seals, sandeels and salmon: Diet of harbour seals in St. Andrews Bay and the Tay Estuary, Southeast Scotland. *Marine Ecology Progress Series*, *390*, 265–276. https://doi.org/10.3354/meps08232

Shelton, A. O., & Mangel, M. (2011). Fluctuations of fish populations and the magnifying effects of fishing. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(17), 7075–7080. https://doi.org/10.1073/pnas.1100334108

Shephard, S., Reid, D. G., Gerritsen, H. D., & Farnsworth, K. D. (2015). Estimating biomass, fishing mortality, and "total allowable discards" for surveyed non-target fish. *ICES Journal of Marine Science*, *72*, 458–466. https://doi.org/10.1093/icesjms/fsu146

Sparholt, H. (1990). An estimate of the fish biomass in the North Sea. *ICES Journal of Marine Science*, *40*(2), 161–172. https://doi.org/10.1093/icesjms/40.2.161

Spitz, J., Mourocq, E., Schoen, V., & Ridoux, V. (2010). Proximate composition and energy content of forage species from the Bay of Biscay: high- or low-quality food? *ICES Journal of Marine Science*, *67*(5), 909–915. https://doi.org/10.1093/icesjms/fsq008

Spitz, J., Trites, A. W., Becquet, V., Cherel, Y., Galois, R., & Ridoux, V. (2012). Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. *PLoS ONE*, *7*(11), e50096. https://doi.org/10.1371/journal.pone.0050096

Stäbler, M., Kempf, A., & Temming, A. (2018). Assessing the structure and functioning of the southern North Sea ecosystem with a food-web model. *Ocean and Coastal Management*, *165*(April), 280–297. https://doi.org/10.1016/j.ocecoaman.2018.08.017

Stienen, E. W. M., van Beers, P. W. M., Brenninkmeijer, A., Habraken, J. M. P. M., Raaijmakers, M. H. J. E., & van Tienen, P. G. M. (2000). Reflections of a specialist: Patterns in food provisioning and foraging conditions in Sandwich Terns Sterna sandvicensis. *Ardea*, *88*(1), 33–49.

Suca, J. J., Wiley, D. N., Silva, T. L., Robuck, A. R., Richardson, D. E., Glancy, S. G., Clancey, E., Giandonato, T., Solow, A. R., Thompson, M. A., Hong, P., Baumann, H., Kaufman, L., & Llopiz, J. K. (2021). Sensitivity of sand lance to shifting prey and hydrography indicates forthcoming change to the northeast US shelf forage fish complex. *ICES Journal of Marine Science*, *78*(3), 1023–1037. https://doi.org/10.1093/icesjms/fsaa251

Sveegaard, S., Nabe-Nielsen, J., Stæhr, K. J., Jensen, T. F., Mouritsen, K. N., & Teilmann, J. (2012). Spatial interactions between marine predators and their prey: Herring abundance as a driver for the distributions of mackerel and harbour porpoise. *Marine Ecology Progress Series*, *468*, 245–253. https://doi.org/10.3354/meps09959

Temming, A., Götz, S., Mergardt, N., & Ehrich, S. (2004). Predation of whiting and haddock on sandeel: Aggregative response, competition and diel periodicity. *Journal of Fish Biology*, *64*(5), 1351–1372. https://doi.org/10.1111/j.0022-1112.2004.00400.x

ter Hofstede, R., & Rijnsdorp, A. D. (2011). Comparing demersal fish assemblages between periods of contrasting climate and fishing pressure. *ICES Journal of Marine Science*, *68*(6), 1189–1198. https://doi.org/10.1093/icesjms/fsr053

Thiel, R., & Knebelsberger, T. (2016). How reliably can northeast Atlantic sand lances of the genera Ammodytes and Hyperoplus be distinguished? A comparative application of morphological and molecular methods. *ZooKeys*, *617*, 139–164. https://doi.org/10.3897/zookeys.617.8866

Tien, N. S. H., Craeymeersch, J., van Damme, C., Couperus, A. S., Adema, J., & Tulp, I. (2017). Burrow distribution of three sandeel species relates to beam trawl fishing, sediment composition and water velocity, in Dutch coastal waters. *Journal of Sea Research*, *127*, 194–202. https://doi.org/10.1016/j.seares.2017.05.001

Tirelli, V., Borme, D., Tulli, F., Cigar, M., Fonda, S. U., & Brandt, S. (2006). Energy density of anchovy Engraulis encrasicolus L. in the Adriatic Sea. *Journal of Fish Biology*, *68*, 982–989. https://doi.org/10.1111/j.1095-8649.2005.00987.x

Troost, K., van Asch, M., Brummelhuis, E., van den Ende, D., van Es, Y., Perdon, K. J., & van der Pool, J. (2021). Centrum voor Visserijonderzoek (CVO) Schelpdierbestanden in de Nederlandse kustzone, Waddenzee en zoute deltawateren in 2020. *CVO Rapport*, 21.001. https://doi.org/10.18174/538895

Troost, K., van Asch, M., Brummelhuis, E., van den Ende, D., van Es, Y., Perdon, K. J., & van der Pool, J. (2024). Centrum voor Visserijonderzoek (CVO) Schelpdierbestanden in de Nederlandse kustzone, Waddenzee en zoute deltawateren in 2024. *CVO Rapport*, 25.008. https://doi.org/10.18174/688163

Tu, C., Chen, K., & Hsieh, C. (2018). Fishing and temperature effects on the size structure of exploited fish stocks. *Scientific Reports*, *8*(7132). https://doi.org/10.1038/s41598-018-25403-x

Tulp, I., Bolle, L. J., & Rijnsdorp, A. D. (2008). Signals from the shallows: In search of common patterns in long-term trends in Dutch estuarine and coastal fish. *Journal of Sea Research*, *60*(1–2), 54–73. https://doi.org/10.1016/j.seares.2008.04.004

Tulp, I., van der Veer, H. W., Walker, P., van Walraven, L., & Bolle, L. J. (2017). Can guild- or site-specific contrasts in trends or phenology explain the changed role of the Dutch Wadden Sea for fish? *Journal of Sea Research*, *127*, 150–163. https://doi.org/10.1016/j.seares.2016.10.001

van Beek, F. (1997). Recruitment surveys on juvenile plaice and sole in continental nurseries in the North Sea by the Netherlands. *ICES Report*, *Y*, 30.

van Bemmelen, R.S.A., Soudijn, F. H., Benden, D., Potiek, A., Chen, C., Hintzen, N., Wilkes, T., van Kooten, T., & Gyimesi, A. (2021). Individual-based model lesser black-backed gulls in the Netherlands. *Bureau Waardenburg Report*, *21–168*.

van Bemmelen, R. S., Leemans, J. J., Collier, M. P., Green, R. M., Middelveld, R. P., Thaxter, C. B., & Fijn, R. C. (2024). Avoidance of offshore wind farms by Sandwich Terns increases with turbine density. *Ornithological Applications*, 126(1)

van Bemmelen, Rob S A, Schekkerman, H., & Fijn, R. C. (2025). Tracking of Black-legged Kittiwakes Rissa tridactyla from an offshore platform in the Dutch North Sea during summer. *SEABIRD*, *37*, 1–21. https://doi.org/10.61350/sbj.37.1

van Bleijswijk, J. D. L., Engelmann, J. C., Klunder, L., Witte, H. J., Witte, J. I., & van der Veer, H. W. (2020). Analysis of a coastal North Sea fish community: Comparison of aquatic environmental DNA concentrations to fish catches. *Environmental DNA*, *2*, 429–445. https://doi.org/10.1002/edn3.67

van der Kooij, J., Scott, B. E., & Mackinson, S. (2008). The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank. *Journal of Sea Research*, *60*, 201–209. https://doi.org/10.1016/j.seares.2008.07.003

van der Molen, J., Ruardij, P., & Greenwood, N. (2016). Potential environmental impact of tidal energy extraction in the Pentland Firth at large spatial scales: Results of a biogeochemical model. *Biogeosciences*, 13(8), 2593–2609. https://doi.org/10.5194/bg-13-2593-2016 167

van der Molen, J., van Leeuwen, S. M., Govers, L. L., van der Heide, T., & Olff, H. (2021). Potential Micro-Plastics Dispersal and Accumulation in the North Sea, With Application to the MSC Zoe Incident. *Frontiers in Marine Science*, 8(607203). https://doi.org/10.3389/fmars.2021.607203

van der Veer, H. W., Creutzberg, F., Dapper, R., Duineveld, G. C. A., Fonds, M., Kuipers, B. R., Van Noort, G. J., & Witte, J. I. J. (1990). On the ecology of the dragonet Callionymus Lyra l. in the southern North Sea. *Netherlands Journal of Sea Research*, *26*(1), 139–150.

van Deurs, M., Christensen, A., Frisk, C., & Mosegaard, H. (2010). Overwintering strategy of sandeel ecotypes from an energy/predation trade-off perspective. *Marine Ecology Progress Series*, *416*, 201–214. https://doi.org/10.3354/meps08763

van Deurs, M., Christensen, A., & Rindorf, A. (2013). Patchy zooplankton grazing and high energy conversion efficiency: Ecological implications of sandeel behavior and strategy. *Marine Ecology Progress Series*, *487*, 123–133. https://doi.org/10.3354/meps10390

van Deurs, M., Grome, T. M., Kaspersen, M., Jensen, H., Stenberg, C., Sørensen, T. K., Støttrup, J., Warnar, T., & Mosegaard, H. (2012). Short- and long-term effects of an offshore wind farm on three species of sandeel and their sand habitat. *Marine Ecology Progress Series*, *458*, 169–180. https://doi.org/10.3354/meps09736

van Deurs, M., & Hartvig, M. (2011). Critical threshold size for overwintering sandeels (Ammodytes marinus). *Marine Biology*, *158*, 2755–2764. https://doi.org/10.1007/s00227-011-1774-8

van Hal, R., Smits, K., & Rijnsdorp, A. D. (2010). How climate warming impacts the distribution and abundance of two small flatfish species in the North Sea. *Journal of Sea Research*, *64*(1–2), 76–84. https://doi.org/10.1016/j.seares.2009.10.008

van Hal, R., Volwater, J., Aarts, G., Brasseur, S., & Glorius, S. (2021). Ecologische effecten van een pilotsuppletie in het Amelander Zeegat: Synthese van onderzoeksresultaten en literatuur. *Wageningen University & Research Rapport*, C004/21. https://doi.org/10.18174/540194

van Keeken, O. A., van Hoppe, M., Grift, R. E., & Rijnsdorp, A. D. (2007). Changes in the spatial distribution of North Sea plaice (Pleuronectes platessa) and implications for fisheries management. *Journal of Sea Research*, *57*, 187–197. https://doi.org/10.1016/j.seares.2006.09.002

van Langevelde, F., Comor, V., de Bie, S., Prins, H. H. T., & Thakur, M. P. (2020). Disturbance regulates the density–body-mass relationship of soil fauna. *Ecological Applications*, *30*(1), 1–8. https://doi.org/10.1002/eap.2019

van Leeuwen, S., Paul, T., Mills, D., & van der Molen, J. (2015). Stratified and nonstratified areas in the North Sea: Long-term variability and biological and policy implications. *Journal of Geophysical Research: Oceans*, *120*, 1–17. https://doi.org/10.1002/2014JC010485

van Rijn, S., & van Eerden, M. R. (2021). Food choice and prey selection by great cormorants Phalacrocorax carbo in a shallow coastal zone in the Dutch delta area: Importance of local flatfish stocks. *Ardea*, *109*(3), 507–528. https://doi.org/10.5253/arde.v109i2.a20

Vrooman, J., von Benda-Beckmann, S., Geelhoed, S., & Lam, F.-P. (2024). Feasibility study for a pilot program: catching and tagging harbour porpoises in the Netherlands. *Wageningen University & Research Report*, C019/24. https://doi.org/10.18174/654100

Walker, N. D., Maxwell, D. L., Le Quesne, W. J. F., & Jennings, S. (2017). Estimating efficiency of survey and commercial trawl gears from comparisons of catch-ratios. *ICES Journal of Marine Science*, *74*(5), 1448–1457. https://doi.org/10.1093/icesjms/fsw250

Wanless, S, Harris, M. P., & Greenstreet, S. P. R. (1998). Summer sandeel consumption by seabirds breeding in the Firth of Forth, south-east Scotland. *ICES Journal of Marine Science*, *55*(6), 1141–1151. https://doi.org/10.1006/jmsc.1998.0372

Wanless, S., Harris, M. P., & Rothery, P. (1999). Intra- and inter-seasonal variation in sandeel, Ammodytes marinus consumption by Kittiwakes, Rissa tridactyla on the Isle of May and longterm changes in numbers, reproductive output and adult survival. *Fisheries Research Services Report*, 12/99

Wanless, S, Harris, M. P., Newell, M. A., Speakman, J. R., & Daunt, F. (2018). Community-wide decline in the occurrence of lesser sandeels Ammodytes marinus in seabird chick diets at a North Sea colony. *Marine Ecology Progress Series*, *600*, 193–206. https://doi.org/10.3354/meps12679

Ward, E. J., Holmes, E. E., & Balcomb, K. C. (2009). Quantifying the effects of prey abundance on killer whale reproduction. *Journal of Applied Ecology*, *46*, 632–640. https://doi.org/10.1111/j.1365-2664.2009.01647.x

Watson, S. C. L., Somerfield, P. J., Lemasson, J., Knights, A. M., Edwards-jones, A., Nunes, J., Pascoe, C., Louise, C., Schratzberger, M., Thompson, M. S. A., Couce, E., Szostek, C. L., Baxter, H., & Beaumont, N. J. (2024). The global impact of offshore wind farms on ecosystem services. *Ocean & Coastal Management*, *249*(107023). https://doi.org/10.1016/j.ocecoaman.2024.107023

Wilson, L. J., & Hammond, P. S. (2019). The diet of harbour and grey seals around Britain: Examining the role of prey as a potential cause of harbour seal declines. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(S1), 71–85. https://doi.org/10.1002/aqc.3131

Windels, K., Brasseur, S., Ransijn, J., Parmentier, B., van Langevelde, F., & Aarts, G. (2026). Grey seal foraging in relation to the tidal, diel and seasonal cycle [Poster session]. *European Cetacean Society*.

Winslade, P. (1974a). Behavioural studies on the lesser sandeel Ammodytes marinus (Raitt) II. The effect of light intensity on activity. *Journal of Fish Biology*, *6*, 577–586. https://doi.org/10.1111/j.1095-8649.1974.tb05101.x

Winslade, P. (1974b). Behavioural studies on the lesser sandeel Ammodytes marinus (Raitt) III. The effect of temperature on activity and the environmental control of the annual cycle of activity. *Journal of Fish Biology*, *6*(5), 565–576. https://doi.org/10.1111/j.1095-8649.1974.tb05100.x

Witbaard, R., Bergman, M. J. N., van Weerlee, E., & Duineveld, G. C. A. (2017). An estimation of the effects of *Ensis directus* on the transport and burial of silt in the nearshore Dutch coastal zone of the North Sea. *Journal of Sea Research*, 127, 95–104. https://doi.org/10.1016/j.seares.2016.12.001

Witbaard, R, Lavaleye, M. S. S., Duineveld, G. C. A., & Bergman, M. J. N. (2013). Atlas of the megabenthos (incl. small fish) on the Dutch continental shelf of the North Sea. *Royal Netherlands Institute for Sea Research*, 1–243.

Witbaard, R., Parmentier, B., & Herman, P. M. J. (2024). Distribution of Sandeel (Ammodytes sp.) in the Dutch North Sea. *Deltares report*, 11210234-000-ZKS-0001.

Witbaard, Rob, Moons, S., Kleine, L., & Craeymeersch, J. (2025). Sedimentary and faunistic effects of medium-deep sand mining along the Dutch Coast. *Estuarine, Coastal and Shelf Science*, *321*, 109337. https://doi.org/10.1016/j.ecss.2025.109337

Wright, P. J., & Bailey, M. C. (1996). Timing of hatching in Ammodytes marinus from Shetland waters and its significance to early growth and survivorship. *Marine Biology*, *126*, 143–152. https://doi.org/10.1007/BF00571386

Wright, P. J., Christensen, A., Régnier, T., & van Deurs, M. (2019). Integrating the scale of population processes into fisheries management, as illustrated in the sandeel, Ammodytes marinus. *ICES Journal of Marine Science*, *76*(6), 1453–1463. https://doi.org/10.1093/icesjms/fsz013

Wright, P. J., Jensen, H., & Tuck, I. (2000). The influence of sediment type on the distribution of the lesser sandeel, Ammodytes marinus. *Journal of Sea Research*, *44*(3–4), 243–256. https://doi.org/10.1016/S1385-1101(00)00050-2

Wright, P. J., Orpwood, J. E., & Scott, B. E. (2017). Impact of rising temperature on reproductive investment in a capital breeder: The lesser sandeel. *Journal of Experimental Marine Biology and Ecology*, *486*, 52–58. https://doi.org/10.1016/j.jembe.2016.09.014

Wright, S. R., Lynam, C. P., Righton, D. A., Metcalfe, J., Hunter, E., Riley, A., Garcia, L., Posen, P., & Hyder, K. (2020). Structure in a sea of sand: Fish abundance in relation to man-made structures in the North Sea. *ICES Journal of Marine Science*, *77*(3), 1206–1218. https://doi.org/10.1093/icesjms/fsy142

Wuenschel, M. J., & Bean, K. A. (2024). Variation in energy density of northwest Atlantic forage species: Ontogenetic, seasonal, annual, and spatial patterns. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, *16*(2), e10287. https://doi.org/10.1002/mcf2.10287

Zuur, A. F., & Ieno, E. N. (2017). Analysis of PMR monitoring data Fisheries effects on marine benthic fauna. *Highland Statistics Ltd.*, 59.

Zuur, A., Ieno, E., & Saveliev, A. (2017). Spatial, Temporal and Spatial-Temporal Ecological Data Analysis with R-INLA. *Highland Statistics* Ltd.

GENERAL SUMMARY

Small (<30 cm) demersal fish, including buried sandeel (despite their usual classification as pelagic species), play an important role as prey for a wide range of predators, such as marine mammals, seabirds, and piscivorous fish. However, significant knowledge gaps remain regarding species-specific spatial distributions, abundances, energetic characteristics, and, specifically for sandeel, diurnal behaviour. Therefore, the primary objective of this thesis is to improve the understanding of these key aspects of prey availability. Accordingly, the main research question guiding this thesis is: **What are the distributional, energetic, and (diurnal) behavioural characteristics of small demersal fish, particularly the two *Ammodytes* species, in the southern North Sea?** An overarching goal is to assess whether the two most abundant sandeel species, *Ammodytes marinus* and *Ammodytes tobianus*, play different roles as prey within the ecosystem.

As outlined in the general introduction (**Chapter 1**), knowledge gaps regarding small demersal fish persist, in part due to the inefficient sampling of standard demersal fish surveys for these species. This is because these surveys are primarily designed to monitor commercially important, larger fish. In addition, demersal surveys aimed at capturing small (juvenile) fish primarily focus on quantifying new year classes in coastal areas and therefore lack sufficient spatial coverage of offshore areas. Similarly, the North Sea-wide sandeel survey (NSSS) also provides limited spatial coverage, with only a few sampling locations in the Dutch North Sea. In this thesis, two alternative sampling methods were therefore used: the Triple-D dredge used by the Netherlands Institute for Sea Research (NIOZ), originally designed for macrobenthos sampling, and the dredge used by Wageningen Marine Research (WMR) to quantify annual trends in shellfish populations. Both gears use fine mesh sizes and cutting blades that penetrate the sediment, making them suitable for capturing small fish, particularly buried sandeel.

In **Chapter 2**, data collected by the Triple-D were analysed to address the spatial distribution of small fish. Biomass distribution maps were created for the most abundant small demersal fish species, as well as for all species combined. The maps covered the Dutch Exclusive Economic Zone and the UK Dogger Bank and were based on 1,307 observations collected between 2006 and 2023. Biomass of all species combined was particularly high on the UK Dogger Bank, with estimates up to 100 g m^{-2}. In the Dutch EEZ, hotspots (<25 g m^{-2}) were located west and north of the Wadden Islands, while lower biomass areas occurred in nearshore regions along the west coast of the Netherlands, the Oyster Grounds, and on the Dutch Dogger Bank. At the species level, dab and plaice showed rela-

tively homogeneous distributions across the study area, whereas dragonet spp., scaldfish, and solenette were more broadly distributed across the entire study area. Goby spp. was restricted to the coastal areas. Sandeel spp. stood out as highly spatially heterogeneous, with locally very high biomass observations. Biomass estimates were further compared with existing trawl-based studies and were found to be at least twice as high as previously reported values. Our estimates of prey biomass may therefore reshape our current understanding of the (prey) carrying capacity of the North Sea ecosystem for predator species.

Chapter 3 addresses the energetic component of the main research question by determining species-specific seasonal calorific energy densities from early autumn to early spring. Clear species-specific over-winter patterns in energy density were observed. Energy densities of dab, dragonet, plaice, and sandeel spp. declined by ~25%, sole by ~10%, while rockling and scaldfish increased by ~10%. Gobies increased from early autumn to early winter before declining, whereas solenette and whiting remained relatively stable. Spring and summer species-specific energy densities were additionally estimated for the two *Ammodytes* species. No significant differences were found between the two *Ammodytes* species, both of which showed a peak in energy density in mid-summer, representing an increase of ~40% from early spring. These results highlight the importance of accounting for seasonal variability in energy density when assessing prey quality. Species-specific end-of-winter energy densities were then applied to convert the biomass estimates from Chapter 2 into species-specific and total energy landscapes. This is important, as prey quality is even more important than prey quantity in predator foraging strategies.

Chapter 4 focuses on the development of species-specific primers for real-time PCR analysis of the three most abundant sandeel species along the Dutch coast (both *Ammodytes* species and *Hyperoplus lanceolatus*). The aim was to enable reliable and cost-effective DNA-based species identification. This is necessary because morphological identification of the two sandeel species is challenging and impossible for severely damaged individuals (a substantial proportion of sandeel collected by a dredge). Yet accurate species identification is essential for understanding their species-specific ecological roles. Morphological characteristics, suitable for large sample sizes, were evaluated by comparison with DNA-based identification. DNA-based identifications were already used to analyse species-specific differences in the energy densities of the two *Ammodytes* species in Chapter 3. In Chapter 5, DNA-based identifications were used alongside morphologically identified species.

Chapter 5 examined the distribution of both *Ammodytes* species in the Dutch coastal zone (<20 nm) to identify species-specific differences in spatial distribution and diurnal behaviour. We analysed seabed data collected during the annual Dutch shellfish survey in spring (2016–2018, 2020–2022). Niche segregation was assessed in relation to depth, sediment characteristics, bivalve biomass, salinity, and temporal variables (day of year and relative time of day). The species showed a largely offshore–nearshore segregation, with *A. marinus* dominant in offshore areas at high abundance, while *A. tobianus* was dominant in nearshore areas. This pattern was largely driven by differences in preferred depth ranges. However, areas where both species co-occurred were also observed, mainly in transition zones between deep and shallower regions. Even within the same sampling hauls they co-occurred. For both species, bivalve biomass was negatively associated with abundance, which suggests that dense bivalve aggregations may hinder burrowing behaviour. Because seabed sampling took place during daytime in spring—the season in which sandeel exhibit their typical diurnal foraging behaviour—we could infer species-specific diurnal behaviour from the data collected in the seabed. Both species showed similar diurnal patterns, with lower seabed densities in the morning, further reduced densities during the day, and a gradual increase towards the highest densities in the evening. Over the sampling period, seabed densities in *A. marinus* increased strongly, while *A. tobianus* showed a more parabolic pattern. The diurnal behaviour of sandeel is an important aspect of their prey availability to predator species, as many predators target sandeel either in the water column (e.g. sandwich terns) or when they are buried in the seabed (e.g. whiting, haddock, harbour porpoise).

Chapter 6 provides a final discussion in which I reflect on and synthesize the insights gained throughout this thesis regarding different aspects of prey availability of small demersal fish to predator species. New research questions are addressed, including suggestions for how to link our results with (top) predators that depend on small demersal fish. This link is crucial, as it provides insight into the functioning of predator species, which are often used as indicators of the ecological state of the Dutch North Sea. A better understanding of prey–predator interactions, including the effects of human interference, can help determine whether management measures (e.g. limiting anthropogenic activities in important foraging areas when these negatively affect either prey or predators) are necessary and effective for improving the ecological status of the southern North Sea ecosystem.

ABOUT THE AUTHOR



Bram was born in Utrecht, the Netherlands, on 24 March 1993. Growing up with nature-loving parents, he spent much of his childhood exploring the natural world, particularly during family holidays in the mountains.

After a brief intermezzo studying a bachelor's degree in Mechanical Engineering at Delft University, a symposium on bio-inspired design made him realise that he was more interested in understanding natural processes than in designing human-made structures. This inspired him to switch to studying Ecology at the University of Groningen. During his bachelor's programme, he spent six months in Bergen, Norway, where a course on salmon aquaculture, sparked his appreciation for applied ecology and his fascination with marine ecosystems.

This led him to pursue a master's degree in Marine Ecology and Aquaculture at Wageningen University. During this programme, he discovered that his greatest scientific interests lay in understanding large-scale natural processes and visualising them through maps—a curiosity perhaps rooted in his love of hiking in remote landscapes. His master's thesis focused on the distribution of thornback ray in the North Sea, followed by an internship at .. National Institute of Water and Atmospheric Research (NIWA) in New Zealand, where he mapped the distribution of hake on the Chatham Rise.

Concerned about the impacts of climate change, Bram subsequently completed a second master's degree in Climate Studies. After graduating from both programmes, he started his PhD at the Royal Netherlands Institute for Sea Research (NIOZ) on Texel. Here he developed a passion for kite surfing, while also investigating the ecology of small demersal fish in the Dutch North Sea, with a particular focus on sandeel.

Currently, Bram continues to work at NIOZ, where he uses and further develops the Triple-D fishing gear to address research questions related to benthic ecosystems. By contributing to the long-term monitoring of benthic life, with a particular interest in sandeel, he aims to improve our understanding of North Sea ecosystems and their responses to climate change and other human pressures.

SCIENTIFIC PUBLICATIONS

Maathuis, M. A., Manche, P., Couperus, B., **Parmentier, B.**, Poos, J. J., Poot, M., Schekkerman, H., Sakinan, S. & Tulp, I. (2025). The small pelagic fish food landscape and its use by common terns Sterna hirundo in the Wadden Sea. *Marine Biology*, *172*(6), 87.

Parmentier, B., Aarts, G., Brasseur, S., Engelhard, G. H., Immler, E., Van Langevelde, F., Tulp, I. & Witbaard, R. (2025). Small fish biomass in the North Sea is far greater than previously estimated. *ICES Journal of Marine Science*, *82*(6), fsaf082.

Staeudle, T. M., **Parmentier, B**., & Poos, J. J. (2024). Accounting for spatio temporal distribution changes in size-structured abundance estimates for a data-limited stock of Raja clavata. *ICES Journal of Marine Science*, 81(8), 1607-1619.

Accepted

Parmentier, B., Brasseur, S., Couperus, B., Immler, E., van Langevelde, F., Perdon, J., Schultz, J., Tulp, I., Witbaard, R., van Zwol, J. & Aarts G. (Accepted) Spatial and temporal niche differentiation of two sympatric sandeel (*Ammodytes*) species. *Marine Ecology Progress Series*

Grey literature

Witbaard, R., **Parmentier, B.** & Herman P. (2024) Distribution of Sandeel (Ammodytes sp.) in the Dutch North Sea. *Deltares rapport*, 11210234-000-ZKS-0001

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in active acoustics. Although this part of the work is not included in this thesis, the research will be continued and will hopefully result in a future publication.

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PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 30 ECTS (= 22 weeks of activities)

Review/project proposal

- Sandeel in the Dutch EEZ | 4.5 ECTS

In-depth / Topical / On-site Postgraduate Courses

- ICES sandeel working group | Copenhagen, Denmark | 2023 | 1.5 ECTS
- Sandeel Workshop | St Andrews, United Kingdom | 2025 | 1.5 ECTS

Methodological / Statistical Postgraduate Courses

- Generalized linear models | PE&RC | 2021 | 0.6 ECTS
- Laboratory Animal Science | WUR | 2021 | 3 ECTS
- Fish module Laboratory Animal Science | WUR | 2021 | 0.6 ECTS
- Bayesian Data Analysis | PE&RC | 2022 | 1.2 ECTS
- Echoview | Echoview | 2022 | 1.5 ECTS

Laboratory training and working visits

- Fishing fieldtrip Stownet Waddenzee | Wageningen marine research | 2021 | 1.5 ECTS
- WBAT (passive acoustic instrument) fieldtrips | Wageningen marine research | 2022 | 0.9 ECTS
- Fish identification course | Wageningen marine research | 2022 | 0.3 ECTS

Invited review of journal manuscripts

- ICES Journal | Demersal distribution and fisheries independent trends of beaked and golden redfish in the Barents and Norwegian Sea | 2025 | 0.5 ECTS

Competence, skills and career-oriented activities

- Efficient Writing Strategies | WUR | 2021 | 1.3 ECTS
- Searching and Organising Literature for PhD | WUR | 2021 | 0.6 ECTS
- Taking charge of your PhD | ElroyCOM Training | 2021 | 0.6 ECTS
- Safety at Sea | DHTC | 2022 | 1.2 ECTS
- Scientific Writing | Taalcentrum VU | 2025 | 1.5 ECTS

Scientific Integrity/Ethics in science activities
- Scientific Integrity | WUR | 2023 | 0.6 ECTS

PE&RC Retreat, PE&RC Day, and other PE&RC events
- PE&RC First year retreat | 2021 | 0.9 ECTS
- PE&RC Last year retreat | 2024 | 0.6 ECTS

National/local scientific meetings, seminars, and discussion groups
- Monthly PhD discussion group | 3 ECTS
- Swimway Science meeting | 2021 | 1.2 ECTS
- Mini Sandeel symposium (organised) | 2022 | 1.5 ECTS
- Netherlands Annual Ecology Meeting | 2022 | 0.6 ECTS
- Zand uit Zee kennissessie | 2022 | 0.3 ECTS
- Noordzee dagen | 2022 | 0.3 ECTS
- Bioacoustic day | 2023 | 0.3 ECTS
- Triliteral Swimway conference | 2024 | 0.6 ECTS
- Swimway end symposium | 2025 | 0.3 ECTS
- WOZEP presentation day | 2025 | 0.6 ECTS
- NWA workshop + proposal 'Knowledge about unprotected species' | 2025 | 1 ECTS

International symposia, workshops and conferences
- Small pelagic conference | Lisbon, Portugal | 2022 | 1.5 ECTS
- FSBI conference | Colchester, United Kingdom | 2023 | 1.5 ECTS
- ICES annual meeting | Newcastle, United Kingdom | 2024 | 1.5 ECTS

Societally relevant exposure
- Interview high school students | 2025 | 0.1 ECTS

BSc/MSc thesis supervision
- Research topic 1: Energie inhoud van zandspiering door middel van verschillende methodes | 3 ECTS
- Research topic 2: Wat is het beste zeehondenvoedsel? | 3 ECTS

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