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ORIGINAL PAPER

The small pelagic fish food landscape and its use by common terns *Sterna hirundo* in the Wadden Sea

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Abstract
Small pelagic fish (SPF) play a vital role in marine ecosystems, transferring energy from plankton to higher trophic levels. However, SPF dynamics in shallow coastal areas are often under-studied, despite their importance as crucial prey near breeding sites of fish-eating birds such as common terns (*Sterna hirundo*). This study had two connected objectives: to map the pelagic fish food landscape in the inlets of the Dutch Wadden Sea and to describe its use by common terns. Two hydro-acoustic fish surveys were conducted in May and October 2022, while tern distribution was assessed using aerial counts and GPS tracking. Prey selection was analyzed through camera traps and DNA analysis of faeces. Herring and sprat were the predominant species in the SPF community, with sandeel also abundant in May. Smelt was most common in freshwater-influenced areas. Most fish were below 12 cm, fitting the preferred size range for common terns. SPF energy density ranged from 20.1 to 22.1 kJ/g dry weight, with sprat having the highest values. SPF biomass showed significant spatiotemporal variability across transects, inlets, and seasons. Common terns foraged frequently around the gullies, feeding mostly on herring. A significant correlation was found between fish biomass and common tern density, indicating food landscape may be a good predictor of tern distribution and vice versa. This study presents the first integrated biomass estimates of SPF in the subtidal areas of Dutch Wadden Sea for both spring and autumn, providing essential data for future energy budget models and management strategies.

Keywords Herring · Sprat · Common Tern · Tidal area · Predator-prey · Energy density

Introduction

The alignment between prey availability for predators and their food requirements is crucial for predator survival and reproduction. Changes in prey availability are a key driver of population declines in various predators, including seabirds feeding on small pelagic fish (SPF) (Cury et al. 2011; Guillemette et al. 2018; Reynolds et al. 2019; Fayet et al. 2021). SPF play a vital role in marine food webs by transferring energy from plankton to larger predators, including birds, sea mammals, and piscivorous fish (Ouled-Cheikh et al. 2022; Ruzicka et al. 2024).

In Europe, studies on the relation between fish and fish-eating birds have traditionally been concentrated around seabird colonies along the coasts of Norway and the United Kingdom (e.g. Furness and Tasker 2000; Frederiksen et al. 2004; Erikstad et al. 2013; Reiertsen et al. 2014). Far fewer studies have addressed the interaction between SPF and piscivorous birds in the Wadden Sea, the largest unbroken shallow system of gullies and intertidal flats globally. The area is particularly renowned for its importance to wading birds, serving as a crucial stopover site for migratory shorebirds along the East Atlantic Flyway (van Roomen et al. 2022). Besides this role as stopover site, the Wadden Sea is

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also an important breeding area for fish-eating seabirds such as the lesser black-backed gull (*Larus fuscus*), sandwich tern (*Thalasseus sandvicensis*), and common tern (*Sterna hirundo*) (Koffijberg et al. 2022). Because they acquire fish by plunge diving, these species rely on fish swimming in the upper water column. They primarily feed on SPF, with abundance and condition of SPF serving as predictors for chick growth and successful breeding (Stienen et al. 2000; Dänhardt and Becker 2011b; Vedder et al. 2019).

Apart from their critical role for birds, SPF also serve as a food source for piscivorous fish such as sea bass (Cardoso et al. 2015) and sea mammals such as the harbour porpoise (Ransijn et al. 2019). SPF are considered high-quality food that cannot easily be replaced by other food types in terms of energy provision (Spitz et al. 2010). Despite their critical role, there is currently no detailed information available on the food landscape of SPF in the entire Wadden Sea, but see Stienen et al. (2000) and (Dänhardt and Becker 2011a) for local studies. Here we define 'food landscape´ as the spatial distribution of SPF as prey for piscivorous birds, including the species- and size composition and their nutritional values. Hence it does not include the actual prey accessibility which is a result of parameters such as vertical distribution of fish in the water column, water transparency, or fish swimming speed.

SPFs are challenging to study in shallow water owing to sampling difficulties, resulting in the fact that coastal areas are under-sampled (Brehmer et al. 2006). Also, SPF are highly mobile and their abundances show highly variable dynamics in space and time (Saraux et al. 2014). Typically, SPF are studied using hydro-acoustic vessel-based surveys, covering large areas along predetermined transects, using acoustic backscatter combined with biological information gained from fishing hauls to estimate fish biomass. However, because these surveys primarily focus on adult SPF stocks, they generally take place in areas deeper than 20 m. The Dutch Wadden Sea, in contrast, serves as a juvenile nursery for SPF and is generally shallower than 20 m (Maathuis et al. 2025). Here, no comprehensive area-wide assessment of SPF biomass has been conducted. Coastal areas are, however, crucial habitats for fish-eating birds because of the vicinity to their breeding locations, especially for central place foragers, that deliver single prey items to their chicks, such as terns (Gochfeld and Burger 1996). Coastal areas are also crucial habitats for fish because they spend their early life stages here, therefore the interaction between fish-eating birds and SPF especially in the shallow coastal areas is still a significant knowledge gap. Without understanding how fish abundance and distribution impact fish-eating birds, it is difficult to explain population trends or evaluate breeding performance. Both are crucial for effective nature management of the Wadden Sea, an area protected under multiple conservation frameworks, including the N2000, UNESCO World Heritage, and the Bonn Convention.

This study addressed two connected objectives: first, to determine the food landscape for birds feeding on SPF, focusing on the temporal and spatial distribution of SPF species, size, biomass and energy density in the subtidal areas of the Wadden Sea; second, to identify the use of this fish food landscape by fish-eating birds, focussing on common terns (*Sterna hirundo*), being one of the most widespread and abundant fish-eating bird species breeding in the region in spring and summer (Manche et al. 2023). We were specifically interested in addressing the following three questions: (i) Which species and sizes contribute to the SPF community in the Wadden Sea, and what is the energy density of the most abundant SPF species? (ii) What is the estimated biomass of small pelagic fish in the inlets of the Dutch Wadden Sea, both in spring and autumn? (iii) How does the distribution of SPF relate to the habitat use and prey choice of fish-eating birds in the Wadden Sea, specifically common terns?

To achieve the objectives of the study, two area-wide hydro-acoustic fish surveys were conducted covering the subtidal areas, one in May– at the start of the tern breeding season, and one in October 2022– as an integration of growth, migration and mortality of SPF populations over summer, but when most terns have left the area after breeding. SPF community composition, size frequency and length-weight relationships were studied, resulting in the first integrated biomass estimation of SPF in the subtidal Dutch Wadden Sea in spring and autumn. Due to the shallow depths, intertidal areas could not be covered by the fish surveys. Furthermore, the energy density of the fish was analysed using calorimetry. The distribution of fish-eating birds was recorded during aerial counts simultaneously with the hydro-acoustic survey in May. Moreover, movements of breeding common terns were assessed using GPS (global positioning system) tracking devices, and their food provisioning was studied using camera traps at nests and by DNA metabarcoding of faeces.

Methods

Study area

The Wadden Sea is a large interconnected system of gullies, intertidal sand flats, mud flats, and salt marshes, along the northern coasts of the Netherlands, Germany and the western coast of Denmark. It is a dynamic system, characterised by strong tidal currents (Maathuis et al. 2024a). Although most of the Wadden Sea is shallow, with depths typically less than 15 m, the inlets between the barrier islands connecting the Wadden Sea to the North Sea are up to 45 m

deep (Fig. 1A). The variations in water depth and current dynamics shape distinct ecotopes, from deep sublittoral zones to supralittoral areas and salt marshes (Baptist et al. 2019; Fig. 1B).

Small pelagic fish

SPF community composition and length distribution

Hydro-acoustic vessel-based surveys were conducted over two periods, from 9 to 19 May 2022 and from 17 to 27 October 2022, across six inlets, moving from west to east: Marsdiep, Vliestroom, Borndiep, Westgat, Lauwers, and Ems-Dollard (Fig. 1A). Due to the practical requirement of a minimum water depth of 5 m for reliable hydroacoustic measurements, the surveys focused on the deeper regions of the inlets. While this limitation meant that the shallow intertidal zones of the Wadden Sea were not represented, the surveys were strategically designed to target large water volumes where the presence of SPF was anticipated. Acoustic data were collected during daylight hours, using a Simrad EK60 echosounder with a 38 kHz and 200 kHz split-beam transducer, fixed to a towed body on the portside of a commercial fishing vessel. The towed body was positioned

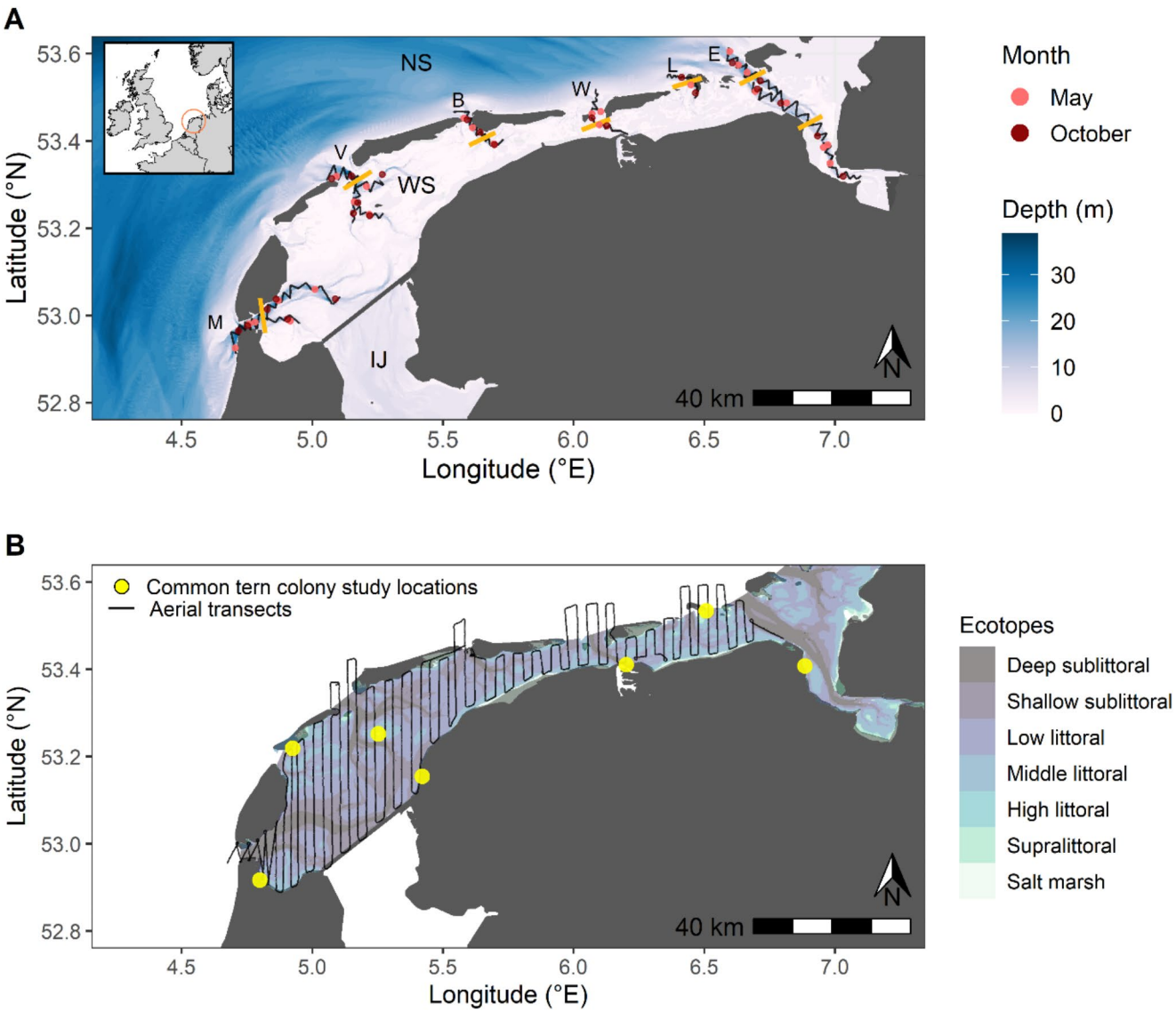


Fig. 1 (**A**) Map of the study area showing the Wadden Sea (WS), North Sea (NS), and the freshwater lake IJsselmeer (IJ), including bathymetry. Black zig-zag lines indicate the acoustic transects, coloured circles represent fish sampling locations, and the six inlets covered by the hydro-acoustic surveys are labelled with their initial letters (M = Marsdiep, V = Vliestroom, B = Borndiep, W = Westgat, L = Lauwers, and E = Ems-Dollard). Additionally, the orange lines indicate the boundary between strata, marking the transition between the landward and the seaward side of the inlets. (**B**) Map of the study area including ecotopes (Baptist et al. 2019). Common tern colony study locations are marked with yellow circles and transects flown during the aerial survey are indicated by black lines

about 1–1.5 m below surface to prevent air bubbles caused by waves from interfering with measurements. Only data from the 38 kHz transducer were analysed for this study, as this is the reference frequency for fisheries surveys (ICES, 2025). Calibration of the acoustic equipment was performed at the start of each survey using a copper sphere (Demer et al. 2015; supplementary Table S1). Zig-zag transects were cruised at a speed of about 13 km/h.

Fishing hauls using a trawl net were conducted to assess fish community composition and size distribution across the six inlets on locations with relatively high amount of backscatter, i.e. fish schools, on the echogram (Fig. 1A). A semi-pelagic otter board trawl net with a 17 m horizontal by 5 m vertical opening and a 10 mm mesh codend lining was used, towed behind the vessel. In total 50 fishing hauls were conducted, each lasting an average of 14 ± 3 min. The vessel maintained a speed of approximately 6 km/h while fishing—balancing engine load, gear performance, and minimizing fish escaping—with an average water column depth of 16.9 ± 6.4 m. Hauls were primarily performed in midwater, at depths between 5 and 10 m, to validate echogram observations and gather biological data. As a cross-check to acoustic densities, haul duration was used to calculate catch per unit effort (CPUE), expressed as fish abundance per minute trawling. From each catch, a subset of fish was measured. Total length was measured to the nearest mm, and individual weights were measured for European anchovy (*Engraulis encrasicolus*), Atlantic herring (*Clupea harengus*), sandeel (*Ammodytes* sp.), European smelt (*Osmerus eperlanus*) and European sprat (*Sprattus sprattus*). No weights were measured for European pilchard (*Sardina pilchardus*), as it was nearly absent in May and not a main prey species for terns. Weight measurements were taken to the nearest 0.5 g in May and 0.1 g in October due to balance availability.

Length-weight relations

Seasonal length-weight relationships of the form $W = aL^b$ were estimated for herring, smelt, sprat, anchovy and sandeel, with parameters *a* and *b* representing the scaling coefficient and allometric exponent, respectively. Parameter estimation was done using linear regression models on log-transformed length L (in cm) and log-transformed weight W (in g), with *a* being the exponent of the regression intercept and *b* being its slope. Although 'mass' is technically more precise, we use 'weight' here to align with standard fisheries terminology. For anchovy and sandeel only few individuals were caught in October, therefore the length-weight relationship could only be estimated for May. The relationships were calculated for the entire size range of fish caught: herring (6–28 cm), sprat (6–14 cm), smelt (6–21 cm), anchovy (7–17 cm), and sandeel (6–18 cm). Since pilchard weights were not measured in our study, Fishbase (https://www.fishbase.se, assessed 10 June 2024) was used to obtain the *a* and *b* parameters in the length-weight relationships for the species. Linear regression models were used to test differences between months. Initially, an interaction between month and length was included. If the interaction was not significant, month was tested as a main effect. Based on the length-weight relationships, mean weights corresponding to each length class per species were calculated.

Biomass estimates

Processing and visualization of acoustic backscatter data were performed using Echoview® 14 (Echoview Software). Acoustic observations between the first 2.0 to 2.4 m below the transducer were excluded due to transducer ringdown effects (Simmonds and MacLennan 2005). Seabed backscatter was excluded with a line positioned 0.4 m above the bottom, which was generated using the 'best bottom candidate' algorithm in Echoview. This line was manually checked and edited, and sections affected by noise were manually excluded. The echograms displayed various aggregations, including small fish schools, individual targets, and a few large schools. These aggregations were collectively used to calculate a numerical fish density indicator: volume backscatter (S_v). Echogram sections that contained acoustic backscatter from fish were isolated using masks to effectively remove background noise and various other untargeted backscatter. Echo integration values, i.e. areal backscatter strength, were then exported per 200 m transect interval (referred to as samples), using a lower S_v threshold of −65 dB re 1 m^2 m^{-3}. This threshold filters out weak signals from non-fish sources, such as gelatinous organisms and small zooplankton, ensuring stronger signals from small pelagic fish are captured (Maathuis et al. 2024a). The nautical area scattering coefficient (NASC in m^2 nmi^{-2}, Maclennan et al. 2002) represents the integrated backscatter from the observed water column, scaled to a square nautical mile area. Samples at the corners of zigzag transects were removed to prevent multiple overlapping observations.

The total distance covered by acoustic measurements in each survey was about 300 km, corresponding to 1550 samples from 144 transects in May and 1682 samples from 151 transects in October. Subsequently, mean NASC values were calculated per transect (see supplementary Figure S1). Transects were assigned to inlets and further divided into 'strata' (Fig. 1A). Two strata were defined per inlet: 'landward' for the side closer to the Dutch mainland and 'seaward' for the side facing the North Sea. The exception was the Ems inlet, which is an estuary and included an additional low salinity stratum called the Dollard.

Trawl fishing data (species composition, length-weight relationships, and length frequency distributions) were used to divide NASC values by species and subsequently calculate fish density and biomass per hectare. Hauls were assigned to strata, excluding 5 of the 50 hauls that were considered not representative— lacking enough small pelagic fish to show a statistically meaningful distribution, for instance due to gear malfunction or poor alignment with echosounder patterns. To calculate the percentage weight contribution of specific species to the total sample, six pelagic fish species were selected: anchovy, herring, pilchard, sandeel, smelt, and sprat. Sandeel comprised two species: lesser sandeel (*Ammodytes tobianus*) and Raitt's sandeel (*Ammodytes marinus*), in approximately a 4:1 ratio. Demersal species that were caught in the trawls (e.g., whiting, plaice) were probably caught due to gear approaching the bottom, thus not representative of the acoustic backscatter in the water column and were therefore excluded. Also, pelagic species such as clupeid post-larvae (< 5 cm), greater sandeel, pipefish, and pencil squid were excluded due to low abundances or weak backscattering properties. For presenting pelagic community composition, percentage weight contribution was averaged by stratum. However, for Westgat and Lauwers, there were not enough representative hauls to divide the inlets into a landward and seaward stratum, so each inlet was treated as a single unit.

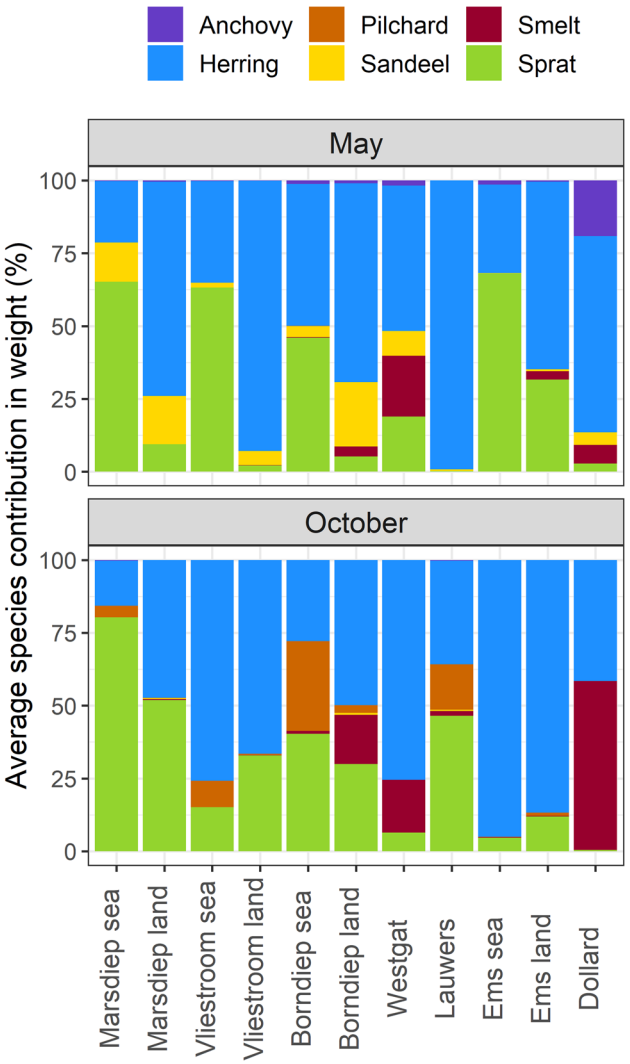


Fig. 2 Average percentage contribution by weight of six small pelagic fish species across different inlets and strata in the Dutch Wadden Sea. The top panel represents data from May 2022, and the bottom panel represents October 2022. Species are differentiated by colour. Inlets on the x-axis are ordered from west to east, and landward ('land') and seaward ('sea') strata are presented if applicable

Using the percentage contribution averaged over strata, NASC values per species per transect were determined for biomass estimation. A correction factor was applied to the weight contribution of sandeel to avoid overestimation, as sandeels lack a swim bladder and do not reflect strongly at 38 kHz (Johnsen et al. 2009; Couperus et al. 2016). Catch data were aggregated per half centimetre class (rounded down to the nearest half centimetre), and the proportion of each species per length class per sample was calculated and averaged over the strata. For herring and sprat, hauls with fewer than 25 individuals of a species were not included in the average, as their length frequencies were not representative. Additionally, for presenting length frequency distributions (Fig. 2), CPUE was calculated using haul duration, expressed as fish numbers per 10 min of trawling. Data were square root transformed, averaged per inlet per season, and then back transformed.

Acoustic target strength (TS), the intensity of the signal returned by a target, per length class was calculated using the TS-length equation: $TS = 20\log(L) - b_{20}$, where b_{20} is a species-specific constant (Foote 1987). For herring and sprat, a b_{20} value of −67.8 dB was applied, suitable for juvenile individuals in relatively shallow conditions (Didrikas and Hansson 2004; Maathuis et al. 2024a). A standard b_{20} value of −71.2 dB, commonly used for clupeids in stock assessments (Lusseau et al. 2023), was used for other SPF species lacking species-specific values. For consistency in comparisons with other studies, calculations for herring and sprat were also conducted using the b_{20} of −71.2 dB.

Subsequently, fish abundance per hectare was determined by computing the area backscattering coefficient (ABC in m²) based on NASC values per length class per species, and further divided by the backscattering cross section (σ_{bs}, the linear equivalent of TS). Biomass was then calculated by multiplying the abundance of fish by the weight per length class and summing across all length classes. This yielded biomass values (in kg/ha) per transect, which were averaged per stratum and inlet. To obtain total pelagic fish biomass, results for all six species were aggregated. Data analysis

was done using R (version 4.3.1) and RStudio (version 2023.06.1).

Energy density

Energy density represents the energy content (in joules) per unit of body mass, reflecting nutritional value. Fish energy density was estimated for herring, sprat, sandeel, and smelt. Herring, sprat, and sandeel were collected in the inlets of the Dutch Wadden Sea during a monthly fishing survey from April to July 2021 (see Maathuis et al. 2025). Smelt were collected during the hydro-acoustic survey in May 2022 (this study). A total of 82 herring, 59 sandeel, 12 smelt, and 78 sprat, ranging in length between 6 and 16 cm, were collected. To measure dry weight, fish were placed in a freeze dryer for a minimum of 3 nights at −50 °C and 0.02 mbar. Subsequently, whole animals (excluding otoliths for sandeels) were ground into powder and compressed into a pill of approximately 0.5 g dry weight. If dry weight of individual fish was less than 0.5 g, benzoic acid was added to reach 0.5 g, with corrections made afterward. The energy density was analysed using an IKAC2000 calorimeter (IKA, Germany). The energy density per g wet weight was calculated using the ratio dry weight to wet weight. Linear regression models were used for each species to test whether energy density varied significantly with fish length. Because significant differences were found for sandeel and smelt, only fish between 10.5 and 13.5 cm were included in the subsequent analysis, which involved a Kruskal-Wallis test followed by pairwise Wilcoxon tests with Bonferroni correction to evaluate interspecies differences.

Subsequently, energy density and biomass estimates were multiplied to estimate the energy available per inlet, specifically calculated here for May, at the start of the common tern breeding season. Biomass values for herring, sandeel, sprat, and smelt in the 4 to 12 cm size range were selected as these were included in the terns' diet (Figure S2).

Common terns

The common tern is a widespread piscivorous bird in the Dutch Wadden Sea. Yet, counts from 1991 to 2017 show an annual population decline of 5% here (Koffijberg et al. 2022). Common terns breed in small to medium-sized colonies, typically ranging from 50 to 500 pairs, with a maximum of 1100 pairs, on islands, saltmarshes, wetlands (both natural and artificial), and flat rooftops behind mainland dykes (Stienen et al. 2009). The breeding season runs from April to July, with the main egg laying period in mid-May for experienced breeders (Ludwigs and Becker 2002) and a chick rearing period of about 25 days from mid-June to mid-July (Becker and Ludwigs 2004). As a central place forager, the species delivers single fish to chicks after foraging trips that can extend several tens of kilometres from the colony (Militão et al. 2023; Kralj et al. 2024).

Counts

To describe the spatial distribution across the Dutch Wadden Sea of (foraging) common terns and other piscivorous birds, aerial transect surveys were conducted on 12 and 13 May 2022, simultaneously with the acoustic fish survey. May falls within the spring migration period for this species, but by the time of the aerial survey, most breeding colonies in the Wadden Sea had already been established. The entire Dutch Wadden Sea was surveyed, except for the Ems Dollard estuary (Fig. 1B). Counts were made from a Cessna 172 aircraft at an average altitude of 75 m, recording the number and behavior of common terns (i.e. flying, foraging and resting). Transects were spaced 2.5–3 km apart, with no overlap between areas counted. Most counts took place around low tide, with wind speeds of 4–5 Bft and minimal cloud cover. The effective strip width, i.e. the perpendicular distance from a transect line taking into account detection loss (Buckland et al. 2015), for common terns was 168 m (Manche et al. 2023). To analyze the relationship between common tern distribution and fish distribution, we created a 168 m buffer around the aerial transects and selected those parts of the buffer that were within 2.5 km of the acoustic fish transects. The number of foraging common terns within these remaining buffers was divided by its area to calculate bird density. This was done per stratum. A linear model was then used to test whether common tern density correlated with fish biomass. Furthermore, ground-based counts of breeding colonies and high-tide roosts of common terns in May and June 2022 were acquired from a standardized long-term bird count carried out by Sovon Dutch Centre for Field Ornithology (Hornman et al. 2012; Vergeer et al. 2023).

Habitat use

During the breeding seasons of 2021 and 2022, a total of 44 common terns from seven colonies (Fig. 1B, range 1–14 terns per colony) were tracked using Pathtrack nanoFix GEO RF tags (3.6 g; Pathtrack Ltd, UK). The tags transmit the data to base stations which were placed in each colony. Adult terns were caught on their nests during the last week of egg incubation, using walk-in traps or spring traps. Tags were attached with a leg-loop harness (total weight 4.1 g), made from 2.5 mm wide 7706-.10" natural tubular spectra tape (Bally Ribbon Mills, USA) in 2021 and from 1.4 mm "original slip elastic" (Preston Innovations, UK) in 2021. The latter option made sure that the tag would fall of the

bird at the end of the breeding season due to deterioration of the elastic.

One tag was lost before data collection began, and the remaining 43 tags provided an average of 27 days of GPS data per tag (range 1–71 days). Fixes were only collected during daytime (04:00–23:00 h) to save battery, as tracks from a previous trial showed no foraging activity during nighttime. Location attempts with less than 4 satellite connections (< 1% of the fixes) were excluded, as these positions were inaccurate. With GPS location intervals of 40 min, individual foraging trips could not be distinguished. Instead, we analysed the distribution of GPS locations per habitat type for each colony, excluding GPS locations inside the colonies. The averages of the habitat distributions were then used as indicator for habitat preference of common terns in the Dutch Wadden Sea. Areas were classified into the North Sea, Wadden Sea, and inland areas (both waterbodies and land), with the Wadden Sea further divided into six ecotopes based on water depth and current dynamics (Baptist et al. 2019; Fig. 1B).

Prey choice

Prey choice, in terms of prey size and type, was studied using two methods: by means of camera traps and by DNA metabarcoding of faeces. Twenty-five camera traps were divided over the seven colonies (Fig. 1B) in 2021 and 2022, one camera per nest per year. The cameras were placed at the ground, approximately 50 cm away from nests, and were triggered by motion detection 24 h per day. They captured images of prey fed to chicks up to 10 days old, as older chicks became too mobile and got out of reach for the cameras. This yielded 1,620 observations of prey, of which species and length were recorded, with prey length measured relative to the adult's bill length (average 3.6 cm; Baker 2016). Identifying prey species from images was challenging due to image quality and small visual differences between species. Herring, sprat and smelt were grouped together as "herring-like" prey items. Additionally, DNA analysis was conducted on tern faeces for detailed prey identification. In June and July of 2022, we collected 25 faecal samples from young chicks (5–12 days old), 25 from older chicks (12 + days), and 1 sample from adult common terns across five colonies. The samples were opportunistically collected during handling and ringing of the birds and stored in 5 ml buffer solutions at room temperature in the dark for at least 48 h. Samples were grouped by colony and age class. DNA metabarcoding was conducted using the MiFish mitochondrial 12S primer (Miya et al. 2020). DNA was extracted using a chloroform-isoamyl alcohol method and PCR amplification was done in triplicate, then pooled and quality-checked. Controls confirmed no significant DNA degradation, contamination or PCR inhibition. Sequencing was performed on an Illumina MiSeq platform (Illumina, UAS) and, along with bioinformatic analysis, conducted by BaseClear (BaseClear B.V., the Netherlands). Bioinformatic analysis was carried out using the MiFish browser-based pipeline (Zhu et al. 2023). Taxonomic classification was performed with BLAST, selecting the top hit based on the lowest E-value and highest sequence identity. Taxonomic assignments were made using the NCBI nucleotide database and manually verified. Read counts per prey type were standardized within each sample by dividing them by the total read count. Identifications with read counts below 1% in a sample were excluded from the analysis. The remaining read counts were then aggregated within each age group, and species with a final read count below 3% were classified as "Other."

Selection of tern colonies

We expected tern foraging behaviour to vary between colonies (Becker and Ludwigs 2004) but had few a priori expectations about the nature of this variation. Therefore, we selected colonies for tagging birds and identifying prey to represent a diverse geographic spread within the Wadden Sea and varying distances to the North Sea. We aimed for an equal distribution, but the final choice of colonies and the number of birds caught, faeces sampled or nests photographed were also influenced by logistical constraints and varying conditions such as site accessibility, ease of capturing birds, and vegetation. GPS tracks were obtained from a subset of birds within a limited number of colonies and were unlikely to capture the full range of foraging locations used by terns breeding in the Wadden Sea, therefore aerial counts were also included to provide a more spatially comprehensive image of their distribution.

Results

SPF community composition

Herring was the most abundant SPF species in the Dutch Wadden Sea, followed by sprat (Fig. 2). In May, there was a difference in the herring-to-sprat ratio between the landward and seaward side of the inlets, with more herring on the landward and more sprat on the seaward side. This pattern was less clear in October, when also sprat contributions decreased towards the east. Sandeel was frequently caught in May, contributing up to 20% in weight, primarily on the landward sides of Marsdiep and Borndiep. Smelt exhibited an easterly distribution in both months, mainly present in the Dollard, Westgat, and landward side of Borndiep. Pilchard was nearly absent in May but was frequently caught

in October, more on the outside of the inlets than on the Wadden Sea side. Anchovy did not substantially contribute to the catch in October but was occasionally present in May, mainly in the Dollard, where it made up 20% of the total weight.

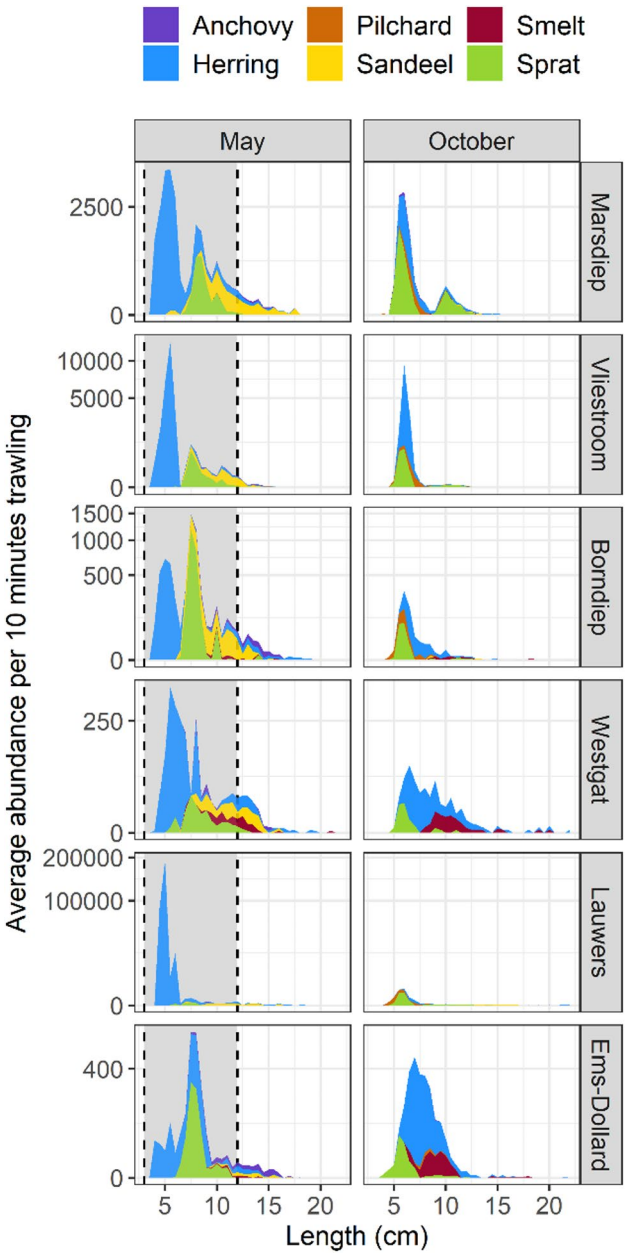


Fig. 3 Cumulative length-frequency distributions of six small pelagic fish species across six inlets in May (left) and October (right) 2022. The inlets are arranged from top to bottom in a west-to-east direction. The Y-axes are square root scaled, representing average catch per unit effort in numbers per 10 min trawling. Species are distinguished by colour. The grey squares indicate the prey size fed to common tern chicks

SPF length distributions

The SPF community in the Dutch Wadden Sea was predominantly composed of small individuals, with most lengths below 12 cm in May and below 15 cm in October (Fig. 3). In May, herring was the smallest SPF species present, peaking in abundance around 5.5 cm, with the highest CPUE in the Lauwers inlet. Sprat abundances peaked around 7.5 cm in size, while length of sandeel, anchovy, and smelt displayed was more variable, ranging from 8 to 15 cm. In October, sprat was the smallest SPF species, though the size differences between species were less pronounced than in May. Sprat showed a main peak in CPUE around 5.5 cm and a smaller peak around 10 cm. Pilchard had a similar size distribution to sprat. Herring averaged around 6 cm, increasing to 7 cm towards the eastern inlets, while most smelt ranged between 7 and 11 cm. In both months, Marsdiep, Vliestroom, and Borndiep exhibited similar length-frequency distributions, while other inlets showed more variation. Generally, the sizes of SPF in the Wadden Sea were similar to the sizes of prey fish fed to common tern chicks, which ranged from 2.7 to 12.6 cm, with a mean size of 5.6 ± 1.7 cm (see supplementary Figure S2).

SPF length-weight relations

Most species exhibited lower weights for their length in October compared to May, suggesting that fish were in slightly better condition in May. Specifically, herring showed this trend most notably between 8 and 20 cm, smelt across the entire range, and sprat from 10 cm onwards (supplementary Figure S3). Sandeel consistently had lower weights for the same lengths compared to other species. The *a* parameter, ranging from 0.002 to 0.008, differed significantly between May and October for herring, sprat, and smelt (Table 1). Additionally, the *b* parameter, which was above 3 for all species except sprat in May, was significantly different for sprat and smelt.

SPF biomass

Herring comprised the highest biomass, particularly in May (Fig. 4). Biomass was generally higher in May than in October, except for smelt. Species distributions varied seasonally; for example, high herring biomass was observed in the Lauwers inlet on the landward side in May, but not in October, and the opposite occurred in sprat. Additionally, sandeel had a clear westerly distribution in May, with biomasses up to 15 kg/ha in the Marsdiep, but its biomass remained below 1 kg/ha everywhere in October. Clear differences were also noted between the seaward and landward side of the inlets in May: sprat was generally more abundant

Table 1 Length-weight relationships ($W = aL^b$) for small pelagic fish in the Wadden Sea, measured in May and October 2022, including sample sizes (n). Linear models tested differences between months, starting with an interaction between month and length. If non-significant, month was tested as a main effect. For anchovy and sandeel, the relationship was only estimated for May due to low October catches

Species	*n*		*P* value interaction	*P* value month	Adj R^2	a		b	
	May	Oct				May	Oct	May	Oct
Herring	324	403	0.9754	< 0.0001	0.99	0.0036775	0.0032747	3.25068	
Sprat	254	226	< 0.0001	< 0.0001	0.95	0.0083651	0.0041255	2.88363	3.199316
Smelt	87	125	< 0.0001	< 0.0001	0.99	0.0041576	0.0020340	3.15730	3.414154
Anchovy	175	5	NA	NA	0.98	0.0027795	NA	3.31147	NA
Sandeel	236	30	NA	NA	0.94	0.0026296	NA	3.04063	NA

on the seaward side of the inlets, whereas herring showed higher biomass on the landward side. Anchovy biomass was below 1 kg/ha in all areas in October, with notable presence in the Marsdiep, Borndiep, and in the Ems-Dollard in May (supplementary Figure S4). In contrast, pilchard biomass remained under 1 kg/ha in May, but showed a clear increase in October, reaching a maximum of 17 kg/ha on the seaward side of the inlets, particularly in the Marsdiep, Vliestroom, Borndiep, and Lauwers (supplementary Figure S4).

In May, total fish biomass decreased from west to east, primarily due to reductions in herring, sandeel, and sprat biomass (Fig. 5, supplementary Table S2). In contrast, smelt biomass generally increased eastward, with the highest values in Westgat and Ems-Dollard. Despite this, Westgat consistently had the lowest biomass of SPF in both months. The mean SPF biomass in May was highest in Marsdiep, followed by Lauwers, Vliestroom, Borndiep, Ems-Dollard, and Westgat, with values of 330, 317, 134, 123, 71, and 17 kg/ha, respectively (supplementary Table S2). Large standard deviations indicated significant variation between transects. Due to their small sizes and low weights, high abundances were observed; for example, in Marsdiep in May, a mean estimated SPF biomass of 330 kg/ha corresponds to 207,495 SPF/ha. In October, the west-east pattern was absent, with all regions showing similar biomass levels, ranging between 11 and 37 kg/ha. When using a TS value of −71.2 dB to calculate biomass for herring and sprat, the biomass approximately doubles (supplementary Table S2).

SPF energy density

The average energy density of SPF in the Dutch Wadden Sea ranged from 20.1 to 22.1 kJ/g dry weight, corresponding to 4.5 to 5.7 kJ/g wet weight (Table 2). Energy density did not differ significantly across lengths for herring and sprat, but did for smelt (linear regression, $p = 0.001$, adjusted $R^2 = 0.064$) and sandeel (linear regression, $p = 0.020$, adjusted $R^2 = 0.076$; Fig. 6A). Energy density of smelt increased with size, while the opposite occurred in sandeel. Sprat showed highest energy density values but also the largest variation. Species differences were significant (Kruskal-Wallis test, $H3 = 26.20$, $p < 0.001$). Pairwise comparisons revealed that herring had significantly lower values compared to the other species (Wilcoxon rank sum test, $p < 0.002$), while no significant differences were observed between the other species. The energy potentially available for common terns in the Wadden Sea during the breeding season, calculated by multiplying energy density by the biomass estimates of suitable species under 12 cm from May, shows a decrease towards the east, with the exception of Lauwers inlet. However, there were substantial variations between individual transects.

Foraging by common terns

During the aerial survey, 531 common terns were counted, of which 40% were foraging (Fig. 7A), 17% were flying, some with fish in their bills, and 43% were resting. Foraging and flying frequently occurred in the studied inlets (note that no bird data is available for Ems-Dollard). Ground-based counts of breeding colonies and high-tide roosts in May and June 2022 indicated circa 4600 common terns in the Dutch Wadden Sea area (Manche et al. 2023). Within the buffer around the fish survey tracks, 124 common terns were counted. A significant correlation was found in May between the density of foraging common terns and that of suitable SPF biomass within the same area (linear regression, $p = 0.0045$, adjusted $R^2 = 0.61$; Fig. 7B). For instance, both the Lauwers landward side and Marsdiep seaward side had high fish biomass and high tern density, whereas Westgat exhibited low densities of both terns and fish.

Examining GPS position data from tracking devices revealed that common terns were often located above or near the major gullies during the breeding season (Fig. 8A and B). On average, deep sublittoral and sublittoral areas accounted for 32.7% of the GPS locations, though this varied by colony. DNA metabarcoding analysis of common tern faeces showed that herring was the primary food given to chicks, regardless of their life stage, followed by sprat, sandeel, gobies (*Gobiidae*), and the freshwater species perch (*Perca fluviatilis*) and bream (*Abramis brama*) (Fig. 8C). The limited sample size prevents drawing definitive conclusions about the adult diet; however, the single adult sample indicated that herring was the primary prey,

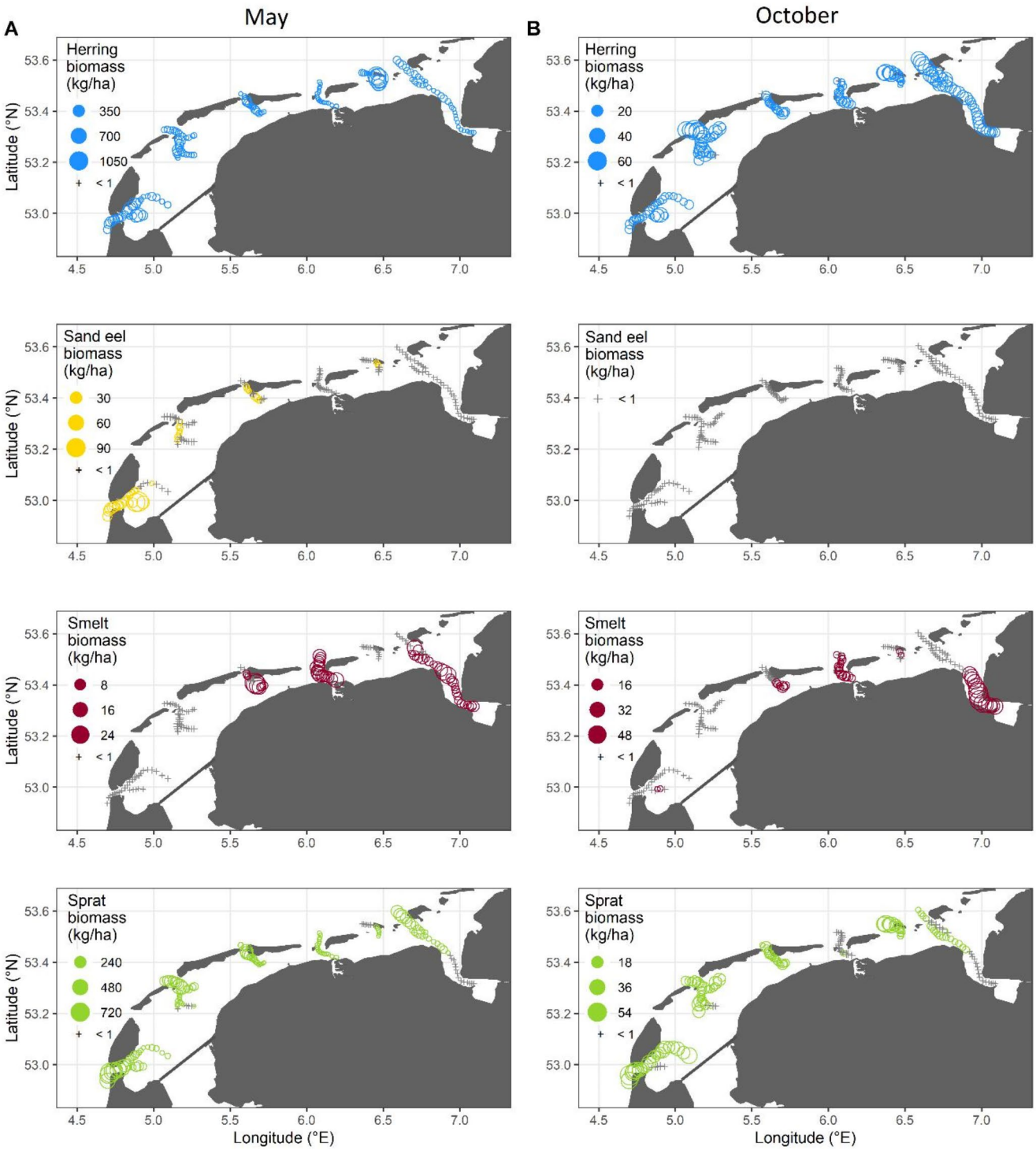


Fig. 4 Distribution of biomass for four species of small pelagic fish in the inlets of the Dutch Wadden Sea in May (**A**) and October 2022 (**B**). The diameter of each circle corresponds to the biomass value in kg/ha, while grey crosses indicate biomass values less than 1 kg/ha. Note the distinct biomass ranges displayed in each plot that differ between species and seasons

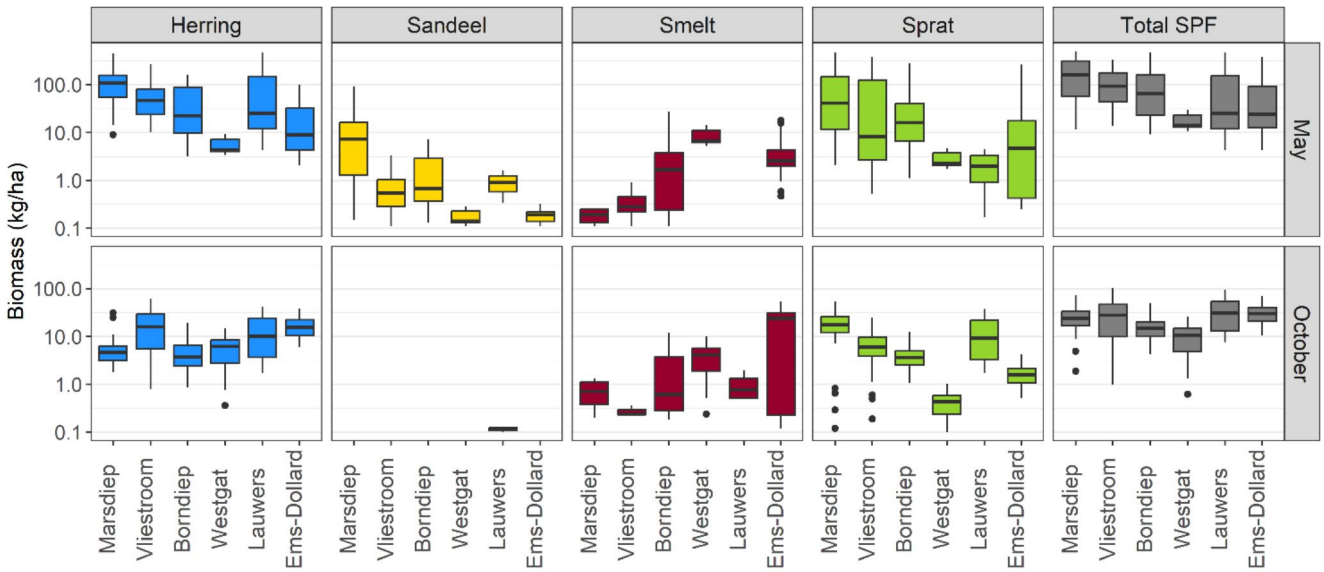


Fig. 5 Biomass (kg/ha) for four species of small pelagic fish (SPF) in the subtidal Dutch Wadden Sea in May and October 2022, along with the total biomass of SPF (pilchard and anchovy included). The inlets are arranged in a west-to-east direction. The observations used for the boxplots are individual samples, the y-axis is logarithmic, and boxes show the minimum, 1st quartile, median, 3rd quartile, and maximum values

Table 2 Energy density (ED, in kJ/g) for dry weight (DW) and wet weight (WW) of four small pelagic fish species in the Dutch Wadden Sea, collected from April to July, with sizes ranging from 6 to 16 cm. Average values are given, including standard deviation and 'n' indicates the sample size

Species	*n*	ED DW (kJ/g)	ED WW (kJ/g)
Herring	82	20.13 ± 1.34	4.52 ± 0.70
Sandeel	59	21.15 ± 0.88	5.29 ± 0.56
Smelt	12	21.88 ± 0.84	4.94 ± 0.44
Sprat	78	22.12 ± 2.33	5.67 ± 1.70

with minor contributions from sprat and sandeel. Camera trap images confirmed the importance of 'herring-like' prey, showing consistent results across both years and all colonies (overall proportion 75%, per-colony range 58–84%, supplementary Figure S5).

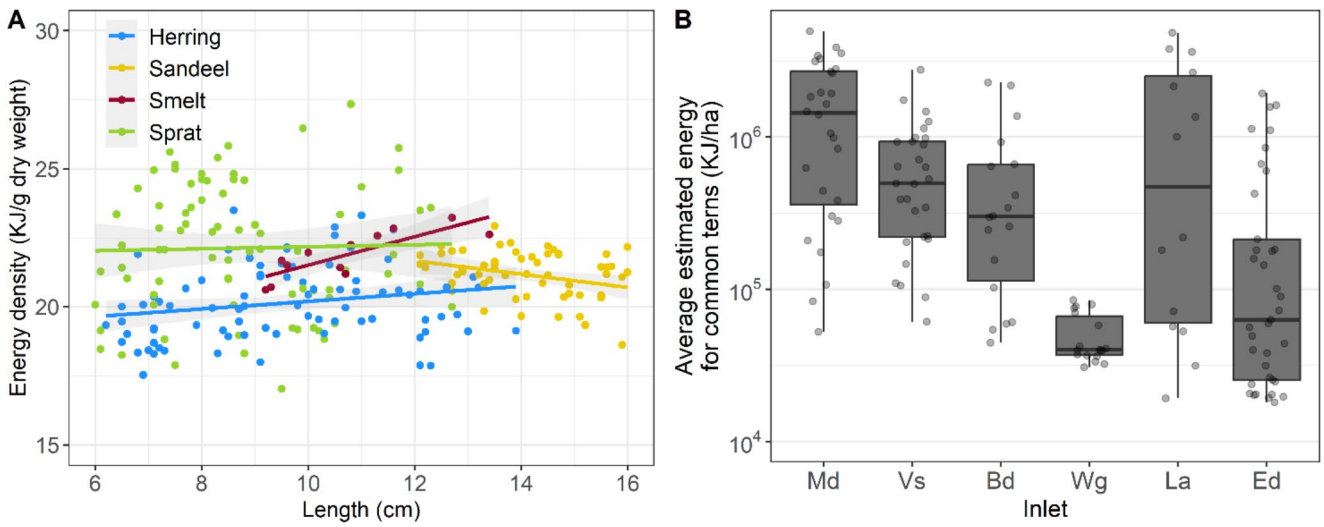


Fig. 6 (**A**) Energy density (kJ/g dry weight) across lengths for four small pelagic fish species. Points represent individual data, and solid lines show linear regression fits for each species, with shaded areas representing 95% confidence intervals. (**B**) Estimated energy of suitable small pelagic fish available for common terns (i.e. herring, sprat, smelt and sandeel below 12 cm) per inlet in the Dutch Wadden Sea. From left to right: Marsdiep (Md), Vliestroom (Vs), Borndiep (Bd), Westgat (Wg), Lauwers (La) and Ems-Dollard (Ed). Note that the y-axes do not start at 0

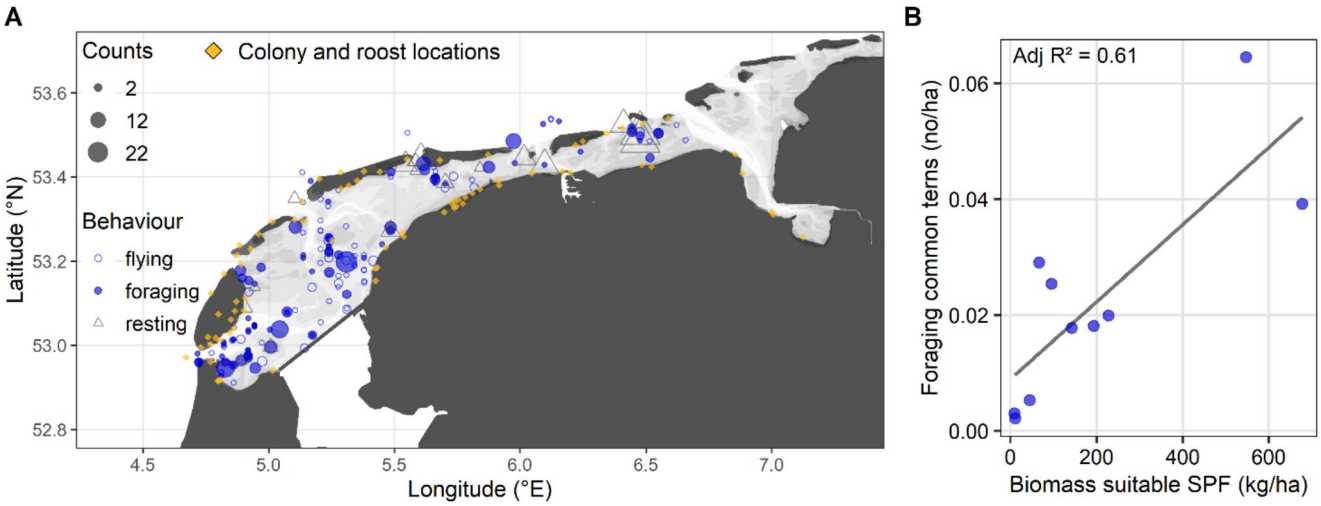


Fig. 7 (**A**) Aerial counts of common terns in the Dutch Wadden Sea in May 2022, categorized by behaviour. Note that the Ems-Dollard inlet was not included in the aerial survey. Colony and high-tide roost locations are marked in yellow. (**B**) Average biomass of SPF suitable for common terns (i.e., herring, sprat, sandeel, and smelt in the 3–12 cm size range) plotted against the density of foraging common terns. Each point represents a stratum and the grey line shows the linear regression

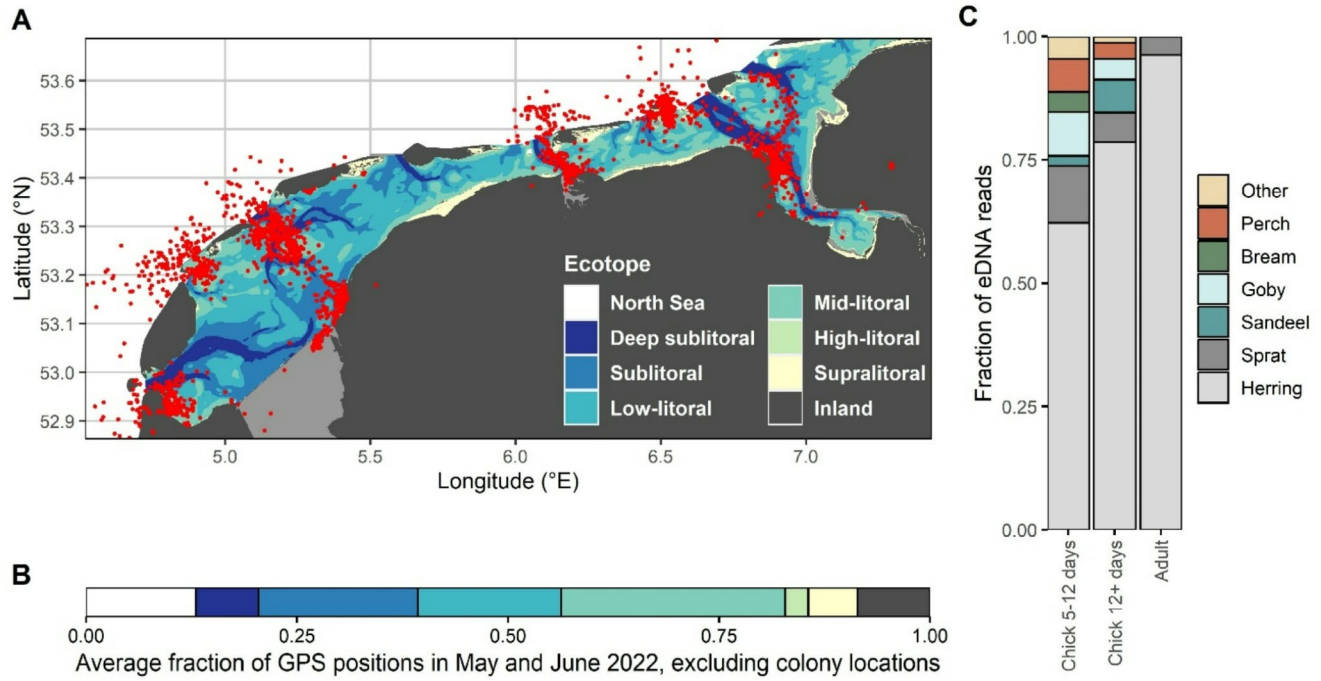


Fig. 8 (**A**) Example of GPS locations of common terns in the Wadden Sea during the breeding season. Per colony, 750 random GPS points of different birds are shown. (**B**) Mean habitat use of all common terns from the seven breeding locations, shown as the fraction of GPS points per habitat, excluding points within the colonies. (**C**) Diet composition of common terns in 2022 determined using DNA metabarcoding analysis of faecal samples, including 25 samples from young chicks (5–12 days old), 25 from older chicks (12 + days old), and 1 from an adult, collected across five colonies

Discussion

By employing a diverse range of techniques, this study addressed the complex task of linking prey distribution and quality to predator distribution and prey choice. This study had two connected objectives: first, to describe the pelagic fish food landscape for birds in the subtidal areas of the Wadden Sea, and second, to describe its use by common terns. Below we first discuss our findings on SPF, then focus on their predators, and conclude with the implications for management.

SPF distribution, biomass and energy density

Acoustic data and targeted trawl catches revealed that herring and sprat dominated the SPF community in the Dutch Wadden Sea, with sandeel being present primarily in May. Smelt was more abundant in the eastern inlets. Additionally, anchovy and pilchard showed lower abundances, and were mainly present in spring and autumn, respectively. Most SPF were smaller than 12 cm, fitting the observed size range for common terns' prey (3–13 cm). SPF biomass showed significant spatial variability both locally (between transects), regionally (between inlets) and seasonally, with a west-east decline in May and a more even distribution in October across all inlets. The fish biomass in May was an order of magnitude larger than in October. Furthermore, the distribution pattern in May showed a distinction between sprat prevailing in the inlets and herring in the Wadden sea proper. While biomass could only be estimated for the subtidal areas of the Wadden Sea due to technical sampling limitations, we believe the information on SPF species composition, size distribution, and energy density is still applicable to the wider area. Furthermore, given that we found terns primarily distributed in the deeper parts of the Wadden Sea, the absence of shallow areas does not substantially impact our key findings.

For the Dutch Wadden Sea, no comprehensive assessment of SPF biomass has ever been conducted. A survey in 1971–1975 using demersal gear, suboptimal for sampling pelagic fish, found more sprat than herring, with greater abundances in spring than in autumn (Dankers and de Veen 1978). In contrast, our current findings indicate higher herring abundance compared to sprat, though autumn biomass remains relatively low, similar to the findings half a century ago (Dankers and de Veen 1978). The lower biomass in autumn is likely driven by large young-of-the-year (YOY, i.e., age 0) mortality and emigration. Additionally, the large annual variability in recruitment observed for most SPF stocks could contribute to these differences, possibly reflecting a good cohort for one species but not the other (e.g. Voss et al. 2012; Burbank et al. 2022). More recently, a study focusing on the western inlet of the Dutch Wadden Sea (Marsdiep) reported clupeid biomass in May ranging from 184 to 411 kg/ha and between 23 and 72 kg/ha in October (Couperus et al. 2016). Additionally, they estimated 9 kg/ha of sandeel in May, compared to none in October. Our results are very comparable (i.e., the same of order of magnitude), considering methodological differences, such as Couperus et al. (2016) using a b_{20} value of −71.2 dB for clupeids. Our biomass estimates are likely conservative for two reasons. Firstly, we used a high b_{20} value (− 67.8 dB, Didrikas and Hansson 2004) in the TS-length relationship to convert acoustic backscatter from herring and sprat into biomass. Published b_{20} values for clupeids are often lower, such as the ICES standard of −71.2 dB used for herring and sprat stock assessments (Lusseau et al. 2023). Because we dealt with juveniles in shallow conditions, we chose −67.8 dB. Using −71.2 dB would have increased biomass estimates by ~54%. Secondly, our acoustic sampling methodology could not sample fish in the top 3–4 m of the water column due to the depth of the towed body and transducer ringdown effects (Simmonds and MacLennan 2005). We observed fish close to the surface, especially in shallower areas, but they were not acoustically detected and thus excluded from the biomass estimate. Stow net sampling of the top 5 m in the German Wadden Sea has shown that sprat, smelt, and herring often occupy surface waters (Dänhardt and Becker 2011a). An alternative approach, using a bottom-mounted echosounder aimed upward, could help detect fish closer to the surface, but even this method misses the upper few meters due to interference from waves (Maathuis et al. 2024a).

Although only two short periods were sampled, we now have a better knowledge about SPF spatial and temporal distribution in the Wadden Sea in Spring and Autumn. The SPF distribution is influenced by environmental factors (e.g. Saraux et al. 2014; Pennino et al. 2020). For instance, SPF distribution is likely linked to the tidal movement of water masses between of the North Sea and Wadden Sea (Couperus et al. 2016). Furthermore, a continuous measuring stationary echosounder in the most western inlet of the Dutch Wadden Sea showed that tidal cycle combined with seasonal effects influenced fish density (Maathuis et al. 2024a). Therefore, the next step would be to assess the drivers behind the spatiotemporal patterns of SPF in the Wadden Sea by conducting repeated, longer surveys including enough resolution in factors such as tide, distance to the North Sea, water transparency, salinity, and temperature.

In addition to prey biomass and distribution, the quality of food is crucial for predators, as it directly impacts their ability to meet energy demands and to reproduce successfully. Energy density, a proxy for prey quality, varies widely among prey species. For forage species in the Bay of Biscay, energy density ranged from 2 to 10 kJ/g wet weight, with SPF considered high-quality prey (Spitz et al. 2010). Species-specific energy density values are needed for bioenergetic models, but they are generally scarce (Johnson et al. 2017; Weil et al. 2019). In our study, we found average energy density values varying between 4.5 and 5.7 kJ/g wet weight, with sprat having the highest caloric value per g but also the largest variation. Despite the general scarcity of energy density values, some data are available for the North Sea (Pedersen and Hislop 2001) and the Wadden Sea (Massias and Becker 1990; Stienen and Brenninkmeijer 2002). Pedersen and Hislop (2001) reported energy density values ranging from 3.9 to 5.2 kJ/g for herring (6–15

cm), 5.8 to 6.4 kJ/g for sprat (4–12 cm), and 6.2 kJ/g for sandeel (12–15 cm). Values that are broadly consistent with our findings, although Pedersen and Hislop (2001) reported slightly higher energy density values for sandeel and sprat. Similarly, Stienen and Brenninkmeijer (2002) found slightly higher energy density values for sandeel compared to our results. Because sandeels have lower energy density than clupeids at equal length, Stienen and Brenninkmeijer (2002) showed that sandwich terns relying solely on sandeels could not provide sufficient energy for their chicks to survive.

Energy density is primarily determined by lipid content, which varies seasonally in herring and sprat (Røjbek et al. 2014). In addition, herring and sprat under 10 cm in the Wadden Sea show seasonal variation in condition, with best conditions found in June (Maathuis et al. 2024b), corresponding with our finding that fish were in slightly better condition in May than in October. We measured energy density from April to July, roughly coinciding with the breeding period of common terns. Therefore, the energy density values for October might differ, but seasonal variations in energy density are typically linked to fish reproductive cycles and hence not so pronounced in small, immature individuals like most SPF in our study (Hislop et al. 1991).

Common terns preying on SPF

Where and when animals forage depends on the spatio-temporal distribution and availability of their prey. The GPS-tracked common terns spent a substantial part of their foraging time above gullies rather than above intertidal areas, unlike black-headed gulls (van Bemmelen et al. 2024). Similarly, the aerial survey showed concentrations of feeding terns near gullies. If we had been able to isolate foraging points from other behaviors in the GPS positions, their preference for inlets would likely be even stronger as most of these locations are quite far from the colony and likely serve as foraging areas rather than transit locations. Furthermore, most of the prey brought to the chicks were herring or sprat. While photos at the nests could not distinguish between the closely related species, DNA analyses revealed that herring was fed to the chicks more frequently, despite sprat's higher energy density. The distribution of sprat further away from the colonies, many of which are located relatively close to or on the mainland, is a likely reason for this discrepancy.

This study used multiple techniques, though not all were applied simultaneously—fish and aerial surveys were conducted in May, while tern diet and tracking data were collected from June to July. This mismatch in timing is suboptimal when comparing food availability for chicks. Our fish study covers the main egg laying period for common terns (Ludwigs and Becker 2002), while the eggs hatch about three weeks later. Chicks require progressively larger fish as they grow (Stienen et al. 2000); therefore, fish of appropriate sizes must be available throughout the chick-rearing period. In mid-May, fish present were mostly below 12 cm, with peaks around 5.5 cm for herring and 7.5 cm for sprat. A monthly study in the same area revealed that by June, herring peak size had increased by approximately one cm, while the peak size for sprat remained similar (Maathuis et al. 2025). Additionally, more YOY herring arrive in the Wadden Sea in June, while the influx of YOY sprat peaks in July (Maathuis et al. 2025). The presence of varying sized fish is crucial for chick development. Larger fish cannot be swallowed well by the smallest chicks, but smaller fish contain too little energy to be profitably transported to chicks except over very small distances, and hence may not allow the parents to supply enough food for optimal growth (Klaassen et al. 1992; Stienen and Brenninkmeijer 2002). In May, all size classes needed for differently aged chicks were present and considering monthly length frequency distributions in Maathuis et al. (2025), this was also still the case in the chick period. Whether or not they were abundant enough requires more intensive field studies consisting of more frequent sampling of both length-structured fish abundance, colony observations of prey delivery by the parents, and reproductive output.

Furthermore, because of the shallow depth in intertidal areas these areas could not be covered by the acoustic survey, so SPF biomass could not be estimated in the intertidal mudflats. Thus, whether SPF remain mainly concentrated in gullies or also inhabit intertidal areas during high tide remains unresolved. Given that forming schools in deeper areas provides protection against predators, it is plausible that SPF concentrated in the subtidal regions. However, to be captured by plunge diving terns, fish need to be available in the upper water layer. Near-surface availability of forage fish may be greatly enhanced by turbulence in the water arising from natural or anthropogenic structures, and terns are known to take advantage of this (Lieber et al. 2021). Similarly, facilitated foraging, where subsurface predators drive forage fish to the surface, can further increase prey availability for seabirds (Maxwell and Morgan 2013).

In Manche et al. (2023), aerial survey data were extrapolated from densities within counted transects to estimate numbers for the entire Wadden Sea. This resulted in an estimate of around 3,200 common terns foraging in the area, closely aligning (115%) with expectations if about half of the breeding population remained at the colony during the survey (Manche et al. 2023). These findings suggest that most terns expected to be foraging were accounted for in the survey, indicating that the majority foraged within the Wadden Sea and its inlets, with little need to infer significant feeding activity in the North Sea or freshwater inland areas.

Notably, breeding stage can influence foraging patterns, as shown in the American Great Lakes, where adult common terns foraged in different locations during incubation and chick-rearing (Bracey et al. 2020). A significant correlation between common tern density and suitable SPF biomass (i.e., herring, sprat, sandeel, and smelt in the 3–12 cm size range) was found, indicating potential fish availability may be a good predictor of tern distribution and vice versa. Studies on piscivorous seabirds demonstrate that spatial scale matters (Fauchald 2009; Fauchald et al. 2011). On a large scale (e.g., North Sea or Wadden Sea wide), seabird distributions are generally linked to prey abundance, as seen in our study. However, on a local scale, SPF distribution may not predict seabird distribution well because of additional (environmental) factors. An important one is prey accessibility, particularly for plunge diving seabirds that can only access the upper half meter of the water column. Unfortunately, acoustic ship-based surveys miss this upper section. However, it was shown in the German Wadden Sea that high SPF densities at greater depths also result in increased SPF near the surface (Dänhardt and Becker 2011a). Factors such as predator presence, water transparency, and SPF abundance likely affect vertical fish distribution and, consequently, prey accessibility to terns (e.g. Maxwell and Morgan 2013; Dänhardt and Becker 2011a). Furthermore, tern distribution is also determined by the location of breeding sites, which are limited to open areas with minimal vegetation and protection from predators.

SPF as a food source in the Wadden Sea ecosystem—management implications

Understanding fish distribution relative to colony distance is crucial for the breeding success of common terns. Our study uniquely integrates data on prey biomass, distribution, length, and energy density with predator distribution and food choice. This information now allows for the calculation of common tern energy budgets, providing insights into suitable breeding locations. Our findings suggest that the greatest potential lies near the outer sections of major gullies, particularly in the western Dutch Wadden Sea.

SPF often exert bottom-up control on predator populations (Cury et al. 2000), therefore this information is also relevant for other predator species. For instance, it was shown that small herring is a key prey species within the Wadden Sea fish community (Poiesz et al. 2020). Furthermore, harbour porpoises (*Phocoena phocoena*) feed on clupeidae and sandeels (Ransijn et al. 2019), while harbour seals (*Phoca vitulina*) primarily eat sandeels and demersal fish, with some herring as well (Kavanagh et al. 2010; Aarts et al. 2019). Additionally, the Wadden Sea also supports large numbers of overwintering piscivorous birds, such as great cormorant (*Phalacrocorax carbo*), Red-breasted Merganser (*Mergus serrator*) and grebes Podicipedidae, which are typically found near the gullies (Schekkerman et al. 2015). While management efforts typically focus on safeguarding higher trophic levels expressed as absolute numbers in e.g. Natura2000 goals, our study underlines that such aims cannot go without a clear understanding of the food landscape available to them. This study provides an image at one point in time of the SPF abundance in the Wadden sea system as a detailed baseline for better understanding of the ecosystem. However, as in the case of most monitoring studies, acoustic surveys can provide a more reliable picture when conducted consistently over a period of multiple years. Therefore, it is essential to continue such monitoring efforts in the area to better resolve the dynamics of the area.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-025-04640-5.

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Author contributions All authors contributed to the study conception and design. Data collection was performed by Margot Maathuis, Bram Couperus, Bram Parmentier and Martin Poot. Analysis was performed by Margot Maathuis, Petra Manche and Serdar Sakinan. The first draft of the manuscript was written by Margot Maathuis, Ingrid Tulp and Petra Manche, all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated and analyzed during the current study are not publicly available, but are available from the corresponding author on reasonable request.

Ethics approval All sampling was performed in accordance with Dutch law concerning animal welfare. The fish protocol was approved by the Animal Ethical Commission of Wageningen UR (experiment code: 2020.D-0026.001; application: 40100202010984). The bird protocol was approved under permit AVD25000202010465.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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