Inter-Research Science Publisher

Marine Ecology Progress Series
Volume 786:meps15143

Published May 28, 2026
https://doi.org/10.3354/meps15143

Opportunistic feeding by a flatfish mesopredator across spatially distinct benthic assemblages — an integrative DNA metabarcoding approach

Eilish M. Farrell[1,*], Ayla Murray[1,2], Birgit Glückselig[1], Manuela Gusky[1], Andrea Desiderato[3], Jennifer Dannheim[4], Jan Beermann[1]

[1]Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Benthic Ecology, Am Handelshafen 12, 27570 Bremerhaven, Germany

[2]Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Arctic Jellies Young Investigator Group, Am Handelshafen 12, 27570 Bremerhaven, Germany

[3]University of Lodz, Department of Invertebrate Zoology and Hydrobiology, Banacha 12/16, 90-237 Lodz, Poland

[4]Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Deep Sea Ecology and Technology, Am Handelshafen 12, 27570 Bremerhaven, Germany

ABSTRACT: Soft-sediment habitats support diverse benthic communities and demersal fish populations, but are facing growing anthropogenic pressures, leading to shifts in predator–prey dynamics. For example, populations of small predators such as the oceanic Lusitanian solenette *Buglossidium luteum* have rapidly increased, with potential impacts on the benthic food web. Stomach content analyses offer a direct way to uncover trophic relationships, but traditional morphological methods can lead to under-representation of certain taxa and an under-estimation of the diet range of small predatory flatfish. Here, we utilized an integrative approach, combining DNA metabarcoding and morphological identification of solenette gut contents collected in the south-eastern North Sea. These observations were further correlated with benthic infauna data of the respective sampling stations. The diet of solenette in the south-eastern North Sea was characterized by a high diversity with a total of 164 different taxa with a clear emphasis on crustaceans and polychaetes across all benthic assemblages in the studied area. However, there was a strong spatial differentiation in prey composition, highlighting solenette as highly opportunistic benthic feeders. DNA metabarcoding detected more prey taxa than morphology alone, highlighting its superior resolution and ability to reveal hidden diet components. The displayed flexibility in the diet of solenette likely contributes to the ongoing success of this flatfish in northern European seas. Consequently, along with warming sea temperatures and the mesopredator release caused by decades of fishing activities, this small benthic predator may exert considerable predation pressure on benthic infaunal communities of the North Sea, with so far unpredictable implications.

KEY WORDS: Predator–prey interactions · Solenette · *Buglossidium luteum* · Mesopredator release · North Sea · Food web · Stomach contents · Demersal fish · Habitat

1. INTRODUCTION

Accurate data of trophic links is central to understanding ecosystem dynamics, and quantifying feeding ecology provides a comprehensive view of species in food webs. In particular, dietary analysis from stomach content across wide spatial scales offers important information on prey distribution and community structure, also supporting ecosystem-based management approaches. In light of ongoing changes in marine ecosystems with regard to function and composition (Möllmann et al. 2015), such basal knowledge is required to predict changes in biological communities. One such example is the German Bight

*Corresponding author: eilish.farrell@awi.de

Publisher: Inter-Research · www.int-res.com

(North Sea), with documented changes as a result of anthropogenic activities impacting both benthic and fish communities (Kröncke et al. 2011, Van Beusekom et al. 2012, Sell & Kröncke 2013, Hiddink et al. 2016, Tiano et al. 2020, 2021). Over the last decades, there has been a noticeable shift in specifically North Sea flatfish communities, from larger, longer-lived species to smaller, faster-growing species that can make use of anthropogenically affected habitats (Fock et al. 2014). For example, plaice *Pleuronectes platessa* and sole *Solea solea* have become less common (Heessen & Daan 1996, Ehrich et al. 1998, Hjermann et al. 2013), while species such as the Lusitanian solenette *Buglossidium luteum* have increased in abundance (van Hal et al. 2010, Fock et al. 2014).

Populations of solenette (family: Soleidae) have expanded in the North Sea, probably due to milder winters, overfishing of its predators and competitors, and its fast growth rate (van Hal et al. 2010, 2016). Once considered rare in mid-20th century surveys (Jiming 1982), it has now become widespread in the German Bight and is often caught as bycatch in trawl fisheries (anecdotal evidence; data lacking due to its non-commercial status). Sonnewald & Türkay (2012) reported solenette with the highest mean species presence index at the Dogger Bank in the North Sea, and it has been detected in environmental DNA (eDNA) surveys widespread across the Sylt Outer Reef and Dogger Bank (Barco et al. 2022). Previous studies have focused on small, localized areas (e.g. Amara et al. 2004, Schückel et al. 2011), overlooking its occurrence across diverse sedimentary and biotic environments in the shallow North Atlantic shelf seas.

Previous surveys on solenette identified a main diet broadly consisting of both benthic macro- and meiofauna (Amara et al. 2004, Schückel et al. 2011); thus, this flatfish likely exerts considerable predation pressure on the benthic communities of the German Bight. However, in order to quantify these effects, both spatially and taxonomically resolved diet data are required. Stomach content analyses across broad benthic habitats provide the best means to directly identify trophic relationships. Traditionally, this method has relied on microscopic examination of stomach contents, but prey items are often damaged, broken down and hard to identify, or rely on hard exoskeletons, reducing the true diet spectrum (Amundsen & Sánchez-Hernández 2019). DNA metabarcoding offers unparalleled taxonomic resolution of dietary components as it allows for the identification of a high number of species, including rare, damaged, and partially digested prey items. It has thus proven useful in the thorough examination of the diet of many fish species (Berry et al. 2015, Günther et al. 2021, Novotny et al. 2022, Underwood et al. 2023, Dischereit et al. 2024b).

The diet of many benthivorous animals can be either opportunistic, driven by the availability of species within benthic habitats (Eggleton et al. 2018, Siegenthaler et al. 2019), or highly specialized (van der Reijden et al. 2018, Heindler et al. 2019). Previous studies indicated that the diet of *B. luteum* is rather broad, which could facilitate its recent range expansion (Nottage & Perkins 1983, Amara et al. 2004, Schückel et al. 2011, 2013). Here, we identified the preferred prey of *B. luteum* across different benthic habitats in the German Bight to elucidate its trophic position. Specifically, we examined stomach contents of this flatfish across spatially distinct benthic assemblages and compared its diet composition with the corresponding infaunal communities. Given previous findings that suggested a broad diet, we hypothesized that *B. luteum* exhibits generalist feeding behaviour across a broad range of benthic habitats. Furthermore, we evaluated the effectiveness of DNA metabarcoding in direct comparison to traditional morphological methods for stomach content analyses.

2. MATERIALS AND METHODS

2.1. Study region

The seafloor of the German Bight encompasses a variety of patchy soft-sediment areas that have been historically characterized by sediment properties, hydrographic conditions, and the inhabiting benthic fauna (Salzwedel et al. 1985, Künitzer et al. 1992, Neumann et al. 2021, Gutow et al. 2022, Beermann et al. 2023). These heterogeneous patch communities have been referred to both from a geomorphological perspective (Gutow et al. 2020) as well as biological perspectives, referring to the dominant biota of the areas, e.g. *Bathyporeia–Tellina* association (Salzwedel et al. 1985, Kröncke et al. 2011).

Specimens of *Buglossidium luteum* were collected during a cruise of RV 'Heincke' in August 2022, from 4 different benthic assemblages corresponding to their known habitat: a sandbank (Dogger Bank), coarse sediment patches in the Sylt Outer Reef, and 2 muddy fine-sand areas of the central German Bight (Fig. 1). As the sediment and hydrography of these areas strongly influences the corresponding benthic community, these 4 different benthic assemblages were named after the dominating sediment class.

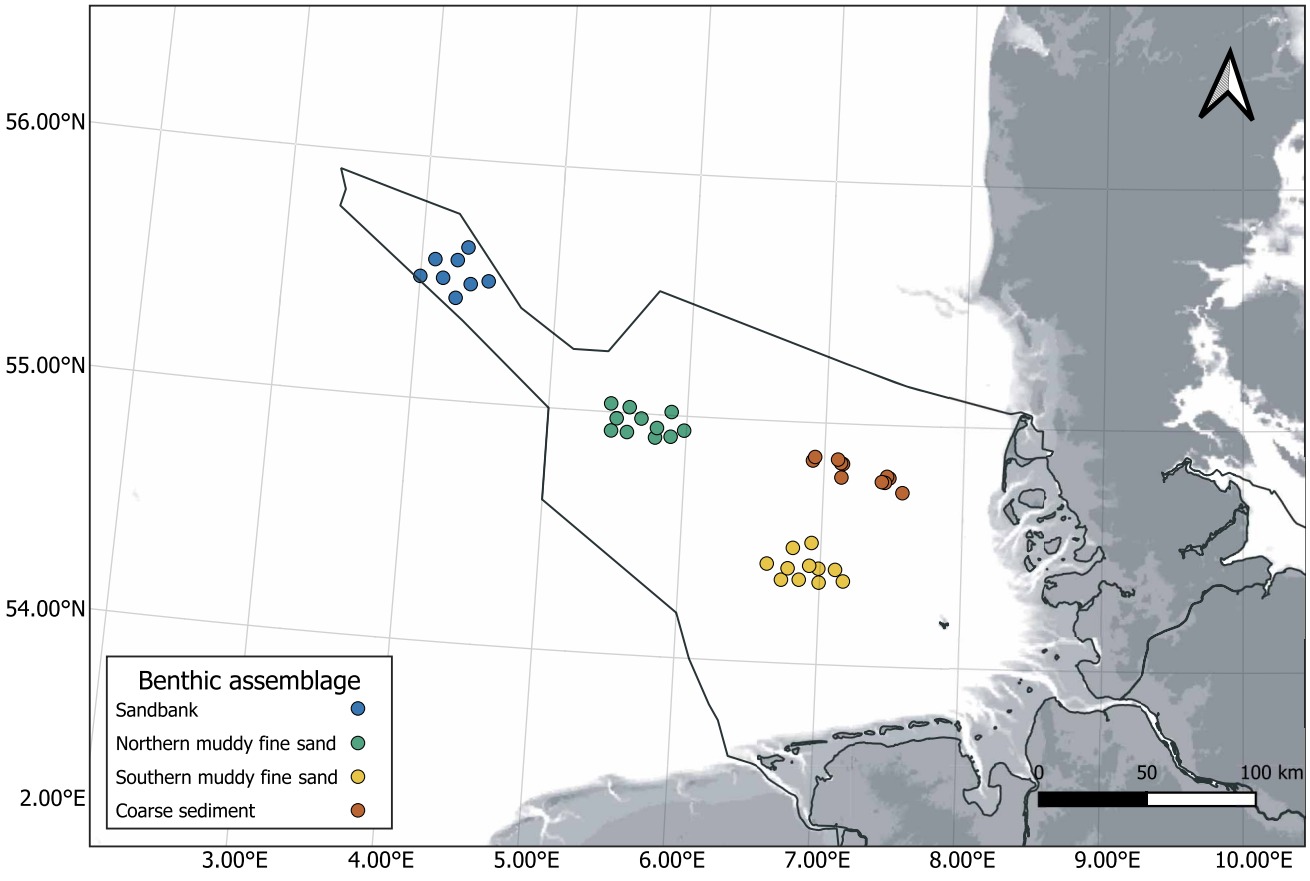

Fig. 1. Sampling area in the German Bight. Points indicate sampling stations. Colour depicts the different benthic assemblages. The German territorial seas are indicated by the black outline

The Dogger Bank is a bathymetric high within the North Sea approximately 30 m below sea level, surrounded by deeper areas of up to 80 m (Stride 1959, Emery et al. 2019). Characteristic benthic fauna here includes the bioturbator *Echinocardium cordatum*, and the polychaetes *Lanice conchilega* and *Spiophanes bombyx* (Beermann et al. 2023). The coarse sediment stations were in an area within the Sylt Outer Reef which are predominantly made up of coarse sand (median grain size >0.5 µm), bivalve debris, and gravel (Diesing et al. 2006, Gutow et al. 2022). They have been previously referred to as the *Goniadella–Spisula* association, due to the characteristic co-occurrence of corresponding polychaetes and bivalves (Salzwedel et al. 1985). The 2 muddy fine-sand assemblages were distinguished primarily by depth and by the relative dominance of overlapping faunal associations. Both areas span elements of the *Fabulina fabula* (formerly *Tellina fabula*) and *Amphiura* associations (Salzwedel et al. 1985), but the northern muddy fine-sand area (>40 m depth) was predominantly associated with *F. fabula*, while the southern muddy fine-sand area (<40 m depth) showed greater dominance of *A. filiformis*. The delineation of these 2 benthic assemblages reflects the transition in depth and faunal composition, with the northern stations also being classed as more diverse than the southern stations (Ducrotoy et al. 2000, Davies et al. 2004).

2.2. Fish and infauna sampling

All samples were collected onboard RV 'Heincke' (cruise no. HE604) in summer 2022 as part of a benthic ecological long-term monitoring programme (on behalf of the German Federal Agency for Nature Conservation [BfN]). At each station, macrofauna was sampled with a van Veen grab (0.1 m^2). Station replicates within each assemblage are shown in Table S1 in the Supplement at www.int-res.com/articles/suppl/meps15143_supp.pdf. The sediment sample was then sieved through a 1000 µm mesh size and the retained fauna were then fixed in a buffered formalin (4%) and seawater solution for storage and transportation back

to the lab facility. Individuals were identified to the lowest taxonomic level possible. Infauna was counted and weighed (wet mass in g), and then stored in 70% ethanol.

B. luteum individuals were collected at each station using an epibenthic dredge (1 m width, 1 cm mesh size) during the daytime. Dredges were towed for 5 min at each station. Fish were immediately frozen at −80°C in individual storage bags to prevent cross-contamination. In the lab, the frozen fish were transferred to freezers and stored at −28°C in order to preserve the gut contents for both visual and molecular methods (Harms-Tuohy et al. 2016, Siegenthaler et al. 2019, Underwood et al. 2023).

2.3. Solenette gut analysis

In the lab, all fish were thawed, and standard (L_S) and total length (L_T) as well as wet weight (g) were measured. For maximum coverage of stomach contents, intact digestive tracts were removed ventrally and included in the analysis, as the intestinal−duodenum combination constitutes the majority of the tract in *B. luteum* (de Groot 1969). The individuals selected for morphological analysis had their stomachs directly analysed after defrosting. Individual fish stomachs for metabarcoding were immediately stored and refrozen whole in sterile Whirl-paks at −28°C for downstream processing.

Solenette individuals were divided for each station between morphological analysis and DNA metabarcoding analysis (Table S1). If only a single *B. luteum* was caught at a station, the DNA metabarcoding method of the stomach contents took precedence. In total, 57 fish stomachs were analysed using DNA metabarcoding, and 38 were analysed using morphological examination.

The collected solenette ranged between 6 and 10 cm total body length (L_T). As solenette are known to mature from 3 yr old, with an L_T between 6 and 7 cm, it was assumed that the collected fish were all mature (Nottage & Perkins 1983, Baltus & Van der Veer 1995, Ellis et al. 2011).

2.3.1. Morphological analysis

The fish chosen for the morphological analysis were defrosted and stomachs were directly analysed. Stomachs were weighed and gut contents were transferred into a petri dish with distilled water to clean and separate contents. All prey items were sorted and identified to the lowest taxonomic level possible under a stereomicroscope (Leica MZ12). Prey was identified following catalogues and keys to the local fauna, as well as expert consultation and comparisons with fresh material. Prey in each group were counted, weighed (wet mass, down to 0.0001 g), and stored in 70% ethanol after investigation.

The morphological stomach content data were curated by removing content such as the mucus remains, foraminifera, nematodes, and noted parasites, in line with the subsequent treatment of gut content data revealed from the metabarcoding method (see Section 2.3.2). Presence of plastic within the guts was also registered, but omitted from the final diet analysis.

2.3.2. Metabarcoding analysis

DNA extraction, library preparation, and sequencing. Stomachs used for metabarcoding were defrosted before DNA extraction. Stomach content was removed into a sterilized plate and homogenized using a small pestle. Contents of visually empty stomachs (mainly mucus) were also extracted, as this still gives reliable results with metabarcoding (Heindler et al. 2019). DNA was extracted from approximately 25 mg of homogenized stomach contents using the DNeasy Blood & Tissue Kit (Qiagen), according to the manufacturer's protocol. The final elution volume was 100 µl. To avoid cross-contamination between extraction of different stomach samples, dissection tools were cleaned with 70% ethanol and thoroughly flame-sterilized between processing of different individuals. Quality and quantity of DNA were checked immediately after extractions by using a Nano-Drop spectrophotometer (Thermo Fisher Scientific), before being stored at −20°C for later analysis.

Extraction of negative controls (blank extractions using only Milli-Q water and no stomach content) were conducted for each extraction event to check for cross contamination.

The 313 bp region of the COI gene was targeted from the extracted DNA, namely the Leray fragment using mlCOIintF-XT (Wangensteen et al. 2018) as the forward primer (5'-GGW ACW RGW TGR ACW ITI TAY CCY CC-3') and jgHCO2198 as the reverse primer (5'-TAI ACY TCI GGR TGI CCR AAR AAY CA-3') (Leray et al. 2013). These primers were chosen as they have already been used to successfully characterize fauna of the North Sea (Barco et al. 2016, Derycke et al. 2021, Mauffrey et al. 2021), fish stomach contents (Leray et al. 2013, Leray & Knowlton 2015, Harms-Tuohy et al. 2016, Novotny et al. 2022, Underwood et

al. 2023), and for other marine metazoan studies (Andújar et al. 2018, Siegenthaler et al. 2019, Dischereit et al. 2024a, Murray et al. 2024). A primer specifically used to avoid amplifying host DNA was not used in this study, as this could reduce amplification of some prey items (Piñol et al. 2014).

Library preparation and sequencing was conducted at All Genetics (www.allgenetics.eu). A 2-step PCR approach was used. In the first amplification step, PCRs were carried out in a final volume of 12.5 µl, containing 1.25 µl of template DNA (diluted 1:5), 0.5 µM of the primers, 6.25 µl of Supreme NZYTaq 2× Green Master Mix (NZYTech), CES 1× (Ralser et al. 2006), and ultrapure water up to 12.5 µl. The reaction mixture was incubated as follows: an initial denaturation step at 95°C for 5 min; followed by 35 cycles of 95°C for 35 s, 55°C for 45 s, 72°C for 45 s; and a final extension step at 72°C for 7 min. Illumina primer sequences were attached in the second PCR using the same conditions as the first PCR, with 5 cycles and different annealing temperature (60°C). Negative controls were included for both PCRs. The library size was verified by running the libraries on 2% agarose gels stained with GreenSafe (NZYTech) and imaging them under UV light. Libraries were purified using the Mag-Bind RXNPure and magnetic beads (Omega Biotek), following the instructions provided by the manufacturer. Finished libraries were pooled in equimolar amounts according to the results of a Qubit dsDNA HS Assay (Thermo Fisher Scientific) quantification (Table S2).

The pool was sequenced in a fraction of a NovaSeq PE250 flowcell (Illumina). Potential traces of adapter dimers were removed using Cutadapt v3.5 (Martin 2011). Quality control of the reads was performed on the forward and reverse reads separately using FastQC (version 0.11.9) (Andrews 2010). Demultiplexing and removal of Illumina adaptors were performed by the sequencing company.

Bioinformatics. Demultiplexed read data were processed via the APSCALE pipeline (version 1.6.3) (Buchner et al. 2022). Forward and reverse reads from each sample were aligned and merged using VSEARCH v2.22.1 (Rognes et al. 2016) (maximum difference percentage = 25, number of maximum differences = 199, and minimum overlap length = 5). Primer trimming was completed using the adapter trimming command in cutadapt (version 4.3, Martin 2011), and high-quality reads were filtered based upon per-base quality and read-length thresholds using VSEARCH (minimum length 303 bp, maximum length 323 bp, allowing for 10 bp error from 313 bp target fragment length). Reads were then dereplicated via the VSEARCH 'fastx_uniques' command. As an abundance quality filtering step, only reads that had an abundance >4 in one sample were retained. As a result, molecular operational taxonomic units (MOTUs) that are represented with more than 4 reads in one sample were kept. Dereplicated reads were all pooled again, and globally dereplicated.

As recommended by Antich et al. (2021), pooled reads were both clustered into MOTUs first, and denoised. Clustering was carried out by VSEARCH with a similarity threshold of 97%. Similarly, denoising was implemented via VSEARCH and using $\alpha = 2$, which corresponds to the number of allowed sequence differences (Edgar 2010). Chimeras were also removed at this stage (via VSEARCH — 'uchime denovo' command). Finally, potentially spurious MOTUs were filtered post clustering using the LULU algorithm (Frøslev et al. 2017). The number of processed reads before and after each step, and all settings used within the APSCALE pipeline, are provided in Tables S3 & S4, respectively.

Taxonomic assignment of MOTUs was performed against the BOLD database v4 (Ratnasingham & Hebert 2007) with the software BOLDigger (version 2.1.2; BOLD accessed on 12 October 2023; Buchner & Leese 2020), allowing for additional utilization of the most recent COI barcodes. Taxonomic thresholds were used following Ershova et al. (2023), i.e. 97% similarity required for species level assignment, 95% for genus, 90% for family, 85% for order, and 75% for class. Flagged hits were individually checked for the degree of uncertainty of a match. The final taxonomic assignment was decided upon by comparing the morphological analysis of other stomachs from similar areas, and from previous studies done on stomach contents of *B. luteum*. Finally, 2 MOTUs were manually changed as a taxonomic assignment was flagged as having 2 or more BOLD entries with differing names above the selected 98% similarity threshold; *Chaetopterus sarsi* was altered to *C. variopedatus*, and *Polybius henslowii* was changed to *P. holsatus*. This was based on the locations of the sampled voucher material, whereby here the taxonomic ID was taken for those specimens sequenced from the North Sea. All taxonomic assignments can be viewed in Table S5.

Data curation. During the final refinement of the data set, a blank correction using the 'maximum contamination' method was conducted. This step removed any read counts within each OTU that are lower than the highest read count within a negative control for that same MOTU (Drake et al. 2022). Next, reads assigned to the host were removed and singletons deleted. Any read counts of less than 5 prey reads within a sample were eliminated, to minimise the risk

of false MOTUs from tag-switching and to reduce noise (Siegenthaler et al. 2019, Antich et al. 2021, Drake et al. 2022, Dischereit et al. 2024b). Sequences were filtered to include only those with a query coverage greater than 85%. Additionally, any reads allocated to MOTUs of terrestrial origin, insects, fungi, phytoplankton, and bacteria were removed from the data set. Reads attributed to a known parasite of *B. luteum, Hysterothylacium aduncum* were also removed from the final data set, yet their presence was still noted across the samples. Nematode sequences were discarded, as it was not possible to delineate parasitic nematodes, or nematodes as secondary prey, from true prey items. Two individuals (Fish 1 and 14) were left with no reads after curation, and were excluded from the analysis.

2.4. Data handling and statistical analyses

Data exploration and statistical analyses were conducted in R version 4.3.2 (R Core Team 2023), with the packages 'vegan' v2.6.4 (Oksanen et al. 2022), 'ggplot2' v3.5 (Wickham 2016), 'phyloseq' v1.46 (McMurdie & Holmes 2013), 'ggVennDiagram' v1.5.2 (Gao et al. 2024), 'car' v3.1 (Fox & Weisberg 2019), and 'microViZ' v0.12.5 (Barnett et al. 2021). Morphological stomach data, metabarcoding stomach data, and benthic infauna grab data were analysed separately and compared descriptively, but were not statistically correlated due to differences in data structure and sampling methodology.

2.4.1. Metabarcoding analysis

Dietary species richness was calculated from rarefied MOTU data using the 'rrarefy' command in the 'vegan' package (Oksanen et al. 2022), to compare diet diversity across benthic assemblages. Differences in species richness across benthic assemblages was compared using the Kruskal-Wallis test (Table S6), followed by Wilcoxon rank-sum tests for post hoc comparisons (Table S7). Both statistical tests were applied using the 'car' package in R (Fox & Weisberg 2019). Further diversity indices (Pielou's evenness and Shannon diversity) were calculated (see Table S8).

Metabarcoding read data were Hellinger-transformed (Legendre & Gallagher 2001, Paliy & Shankar 2016), and Bray-Curtis dissimilarities were calculated to create 2-dimensional nMDS ordination plots to investigate differences in diet composition. Groups were identified using 95% confidence ellipses, assuming a multivariate *t*-distribution. PERMANOVA was then applied, with the benthic assemblage as the main factor in the model, to identify significant differences in diet. Homogeneity of dispersion was tested using ANOVA and the betadispers function ('vegan' package) prior to conducting a PERMANOVA (Table S9), and assumptions were met. Pairwise testing was carried out with the 'pairwise.adonis' function from the 'pairwiseAdonis' package in R (Table S10; Martinez-Arbizu 2020), with Holm adjusted p-values (Dunn 1961). To visualize prey dominance, reads were transformed to semi-quantitative relative read abundance (RRA) within each benthic assemblage.

2.4.2. Morphological analysis

Morphologically identified stomach content data were analysed using the frequency of occurrence metric (%FOO), which accounts for biases introduced by variable digestion affecting prey size and number (Baker et al. 2014, Traugott et al. 2021). Frequency of occurrence was calculated following Amundsen & Sánchez-Hernández (2019) as:

$$f_i = \frac{N_i}{N} \quad (1)$$

where N_i is the number of fish stomachs with prey type i, and N is the total number of fish stomachs containing prey. Values were expressed as percentages and calculated separately for each of the 4 assemblages. For the %FOO of lowest taxonomically identified prey items across the whole data set, see Table S11.

Due to digestion-related biases and smaller sample sizes, statistical analyses were restricted to presence–absence data at the lowest taxonomic resolution possible for each individual solenette. Dietary variation among benthic assemblages was visualized using a non-metric multidimensional scaling (nMDS) ordination plot based on Jaccard distances. Permutational multivariate analysis of variance (PERMANOVA) analysis (9999 permutations) was subsequently used to identify if prey groups at the lowest identified taxonomic level and the benthic assemblage were significant factors (Table S12). A post-hoc pairwise adonis test was performed to investigate differences between groups (Table S13).

2.4.3. Benthic infauna analysis

As a van Veen grab targets macrofauna, and DNA metabarcoding data are semi-quantitative and target

all distinct taxonomic units, prey abundance in the field was not statistically correlated with dietary data. Here, we opted for Ivlev's electivity index (*E*) (Ivlev 1962) to assess relative prey selection, following previous applications in similar studies (Schückel et al. 2013, 2024, Barrera-Oro et al. 2019, Schaafsma et al. 2024). Fish caught in grabs were additionally removed from the benthic fauna data. Ivlev's electivity index (*E*) was calculated per benthic assemblage, as follows:

$$E = (r_i - p_i) \times (r_i + p_i)^{-1} \quad (2)$$

where r_i is the relative read abundance of prey species i in the stomachs, and p_i is the relative abundance of prey species in the field per m^2, respective to each benthic assemblage. The index was adapted for this study by utilizing only relative read abundance of prey items from metabarcoding data rather than visual abundance estimates. The relative abundance of morphologically identified prey was not used, as the taxonomic resolution was too variable. Similarly, the closest taxonomic rank was used to match the RRA dietary item with the infaunal grab data (e.g. genus-level matching for swimming crabs *Polybius* spp.). Ivlev's index provides a rank order of the prey selection rather than a quantitative comparison (Jacobs 1974). Values can range from −1 (inaccessible prey or avoidance), to +1 (selection or readily available prey). Non-selective feeding is illustrated with values centred around 0. The index was calculated only for the top 10 prey items from each benthic assemblage, and discussed (Table 1).

Observed infaunal species richness across assemblages was compared using the Kruskal-Wallis test (Table S14), followed by Wilcoxon post hoc comparisons (Table S15) (Fox & Weisberg 2019). Overlap between infaunal communities and diet composition was assessed with Venn diagrams using the 'ggVennDiagram' package (Gao et al. 2024), identifying shared and unique taxa between stomach content and grab samples.

3. RESULTS

3.1. Prey diversity across benthic assemblages

A total of 3 165 880 reads were recovered after sequencing, with 37.5% assigned to the host, *Buglossidium luteum*. From these reads, 164 MOTUs were assigned to 10 phyla, 38 orders, 87 families, 100 genera, and 113 species after the various bioinformatic steps. The negative controls contained very little to almost no DNA (Table S2). Rarefaction curves

Table 1. The 10 most abundant molecular operational taxonomic units (MOTUs), based on unrarefied relative read abundance (RRA, %) of *Buglossidium luteum* diet within each benthic assemblage. Prey electivity (*E*), calculated from Ivlev's electivity index, is also displayed. Positive *E*-values indicate selection or accessible prey, negative values indicate inaccessible prey or avoidance, and values around 0 indicate non-selective feeding. If an 'x' is displayed, the prey item was not found in the corresponding infauna data of the benthic assemblage

Sandbank			Northern muddy fine sand			Southern muddy fine sand			Coarse sediment		
Species	RRA (%)	*E*	Species	RRA (%)	*E*	Species	RRA (%)	*E*	Species	RRA (%)	*E*
Bathyporeia guilliamsoniana	47.31	+0.94	*Polybius holsatus*	28.22	+0.97	*Polybius holsatus*	31.81	+0.98	*Spio* spp.	27.62	+0.87
Longipedia spp.	14.26	x	*Bathyporeia tenuipes*	9.49	+0.87	*Sthenelais limicola*	9.94	+0.89	*Lanice conchilega*	22.54	+0.76
Spiophanes bombyx	6.10	−0.76	*Harpinia antennaria*	8.98	+0.70	*Bathyporeia tenuipes*	9.19	+0.94	*Gastrosaccus spinifer*	9.03	+0.23
Bathyporeia spp.	5.98	+0.95	*Diastylis laevis*	5.47	+0.85	*Polybius depurator*	8.48	+0.93	*Polybius holsatus*	8.11	+0.83
Argissa hamatipes	2.85	+0.88	*Gattyana cirrhosa*	5.23	+0.76	*Processa modica*	6.17	+0.95	*Eumida mackiei*	5.05	+0.88
Philine indistincta	2.24	+0.90	*Harmothoe glabra*	4.98	x	*Diastylis laevis*	5.91	+0.93	*Philocheras*	3.55	+0.88
Microprotopus maculatus	1.20	x	*Pariambus typicus*	4.98	x	*Limanda limanda*	3.74	x	*Diastylis laevis*	2.76	+0.85
Ectinosomatidae	1.86	x	*Longipedia* spp.	4.93	x	*Processa nouveli holthuisi*	2.75	+0.79	*Crangon crangon*	2.66	+0.85
Scolelepis bonnieri	1.84	+0.83	*Sthenelais limicola*	4.47	+0.66	*Longipedia* spp.	2.71	x	*Gyptis* sp.	2.57	x
Leucothoe incisa	1.82	+0.79	*Polybius depurator*	4.09	+0.83	*Leucothoe incisa*	1.97	+0.79	*Philocheras trispinosus*	2.01	+0.80

(Fig. S1) approached asymptotes in nearly all samples, demonstrating that sequencing depth was adequate to capture the majority of dietary MOTUs.

The highest MOTU richness in fish diets was detected within the Phylum Arthropoda (69 MOTUs, all belonging to the Crustacea), followed by Annelida (48) and Mollusca (20). Crustacean prey occurred in all benthic assemblages. The lowest MOTU richness was found within Chaetognatha and Phoronida, each represented by a single MOTU in stomach contents (*Sagitta* sp. and *Phoronis muelleri*, respectively).

Dietary prey richness differed significantly between benthic assemblages (Fig. 2A, Kruskal-Wallis: χ^2 = 34.52, df = 3, $p < 0.0001$). Solenette from the northern muddy fine-sand assemblage exhibited more diverse diets (Fig. 2A, Wilcoxon test: each $p < 0.05$) compared to sandbank and coarse sediment. In contrast, diet richness from the southern muddy fine-sand assemblage did not differ significantly from the northern muddy fine-sand assemblage (Fig. 2A, $p = 0.121$).

In direct comparison, species richness of the field infauna also varied significantly amongst the benthic assemblages (Fig. 2B, Kruskal-Wallis: $\chi^2 = 30.56$, df = 3, $p < 0.0001$, Table S14). Benthic infaunal diversity was highest on the sandbank assemblage and differed significantly from all other assemblages (Fig. 2B, Wilcoxon tests: each $p < 0.0001$, Table S15).

3.2. Prey composition from metabarcoding analysis

Diet composition from metabarcoding revealed pronounced differences between benthic assemblages (Fig. 3, Table 1). Sandbank diets were dominated by amphipods (Fig. 3), particularly the species *Bathyporeia guilliamsonia* (47.31% RRA; Table 1), with numerous other amphipod taxa occurring exclusively there (Table S12). The gastropod *Hermania indistincta* was the only dominant mollusc in the solenette diet, also from the sandbank assemblage.

Solenette from coarse sediment assemblages had mainly consumed polychaetes (Fig. 3), especially *Spio* spp. (27.62% RRA; Table 1). In addition, the shrimps *Philocheras trispinosus* and *Crangon crangon,* as well as mysids, were also noted more frequently in diets from coarse sediments compared to other assemblages (Fig. 3).

In muddy fine-sand assemblages, diets of solenette were characterized by a high contribution of swimming crabs, with *Polybius holsatus* being ubiquitous and particularly abundant (Table 1). Fish prey, i.e. dab *Limanda limanda* and lyre fish *Callionymus lyra*, also occurred exclusively in diets from the muddy fine-sand assemblages. *L. limanda* represented a dominant prey item in the southern muddy fine-sand assemblage (3.74% RRA; Table 1). The swimming crab *Polybius pusillus* appeared only in stomachs from the southern muddy fine-sand assemblage, while the ghost shrimp *Callianassa subterranea* was unique to fish stomachs from the northern muddy fine-sand assemblage.

Overall diet composition of *B. luteum* differed significantly among assemblages (Table S10, PERMANOVA: pseudo-$F_{3, 53} = 7.74$, $p = 0.001$), with all pairwise comparisons being significant (Table S11, $p < 0.05$). The ordination plot revealed clear separation between the coarse sediment and sand bank diets (Fig. 4A), with considerable overlap between diets from the muddy fine-sand assemblages (Fig. 4A).

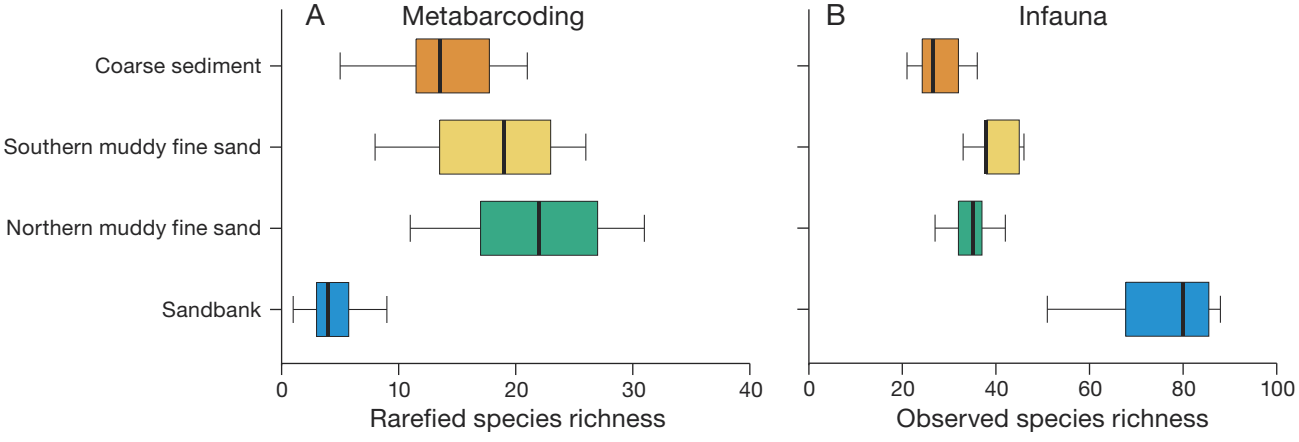

Fig. 2. (A) Rarefied species richness of normalized operational taxonomic unit (OTU) prey within each benthic assemblage, in direct comparison with (B) the observed species richness of the benthic infaunal data from the same sampled stations in the field. The boxes show the lower and upper quartiles, the thick black line within the box depicts the median, while the whiskers extend to the maximum and minimum values

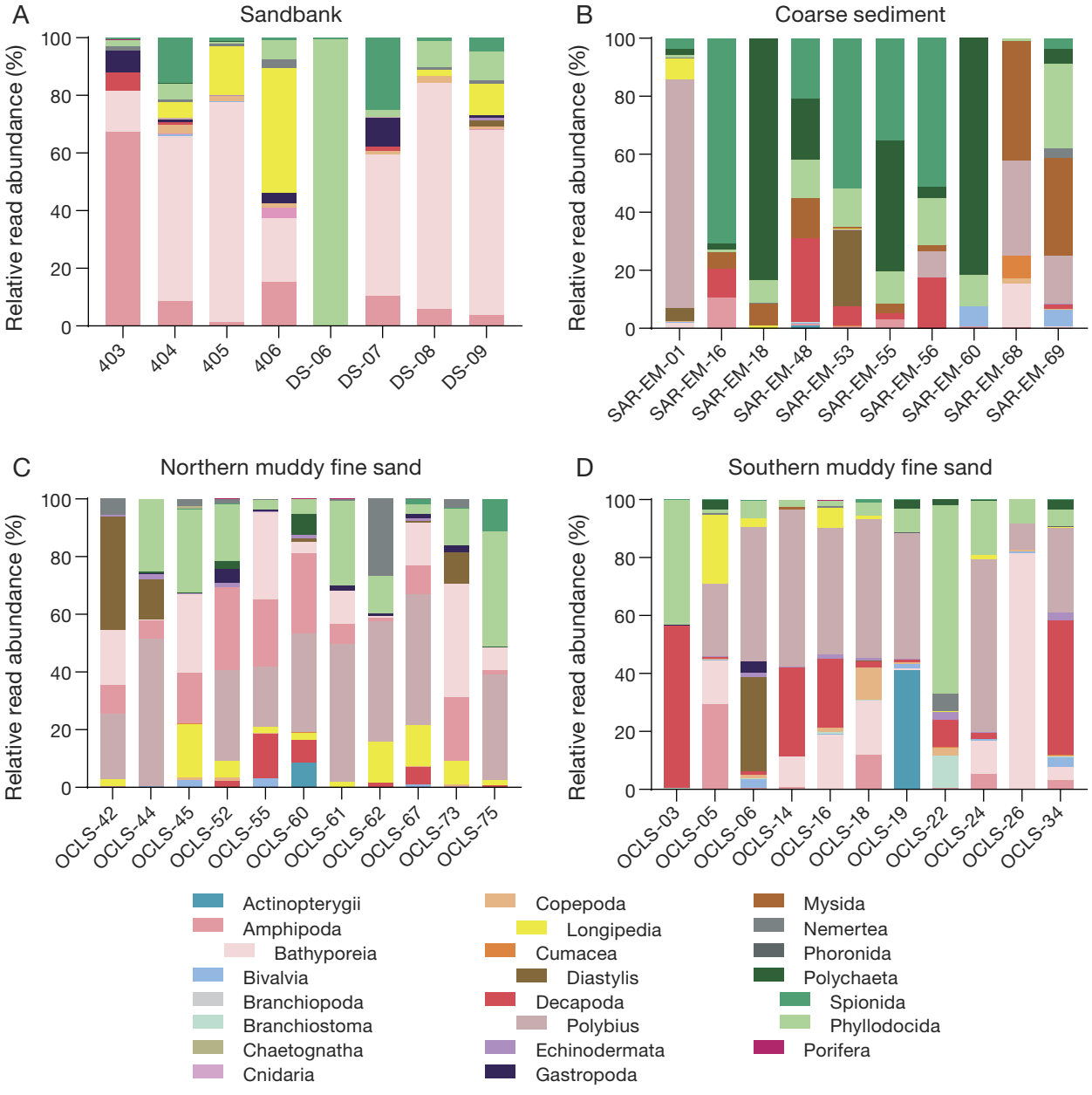

Fig. 3. Relative read abundances (RRA, %) of prey items found in the stomach contents of *Buglossidium luteum* from the (A) sandbank, (B) coarse sediment, (C) northern muddy fine-sand, and (D) southern muddy fine-sand assemblages. For visual purposes, prey species are grouped into ecologically relevant groups to enhance prey differences between stations. Bars represent fish prey sampled from each distinct station, within each assemblage

3.3. Prey composition from morphological analysis

The gut content of *B. luteum* was heavily fragmented and characterized by the presence of sand grains across all analysed individuals. Crustaceans (mainly Malacostraca and Copepoda) dominated across all benthic assemblages. Details on all lower taxonomic levels are provided in Table S11.

The solenette diet in muddy fine-sand assemblages was characterized by a high contribution of swimming crabs (Polybiidae, predominantly *Polybius* spp.), which dominated both the northern (66.66%) and southern (69.23%) muddy fine-sand assemblages (Table 2). Bivalves, primarily from the family Cardiidae, were also common in muddy fine-sand diets (Table 2). Polychaetes were restricted to the families Spionidae and

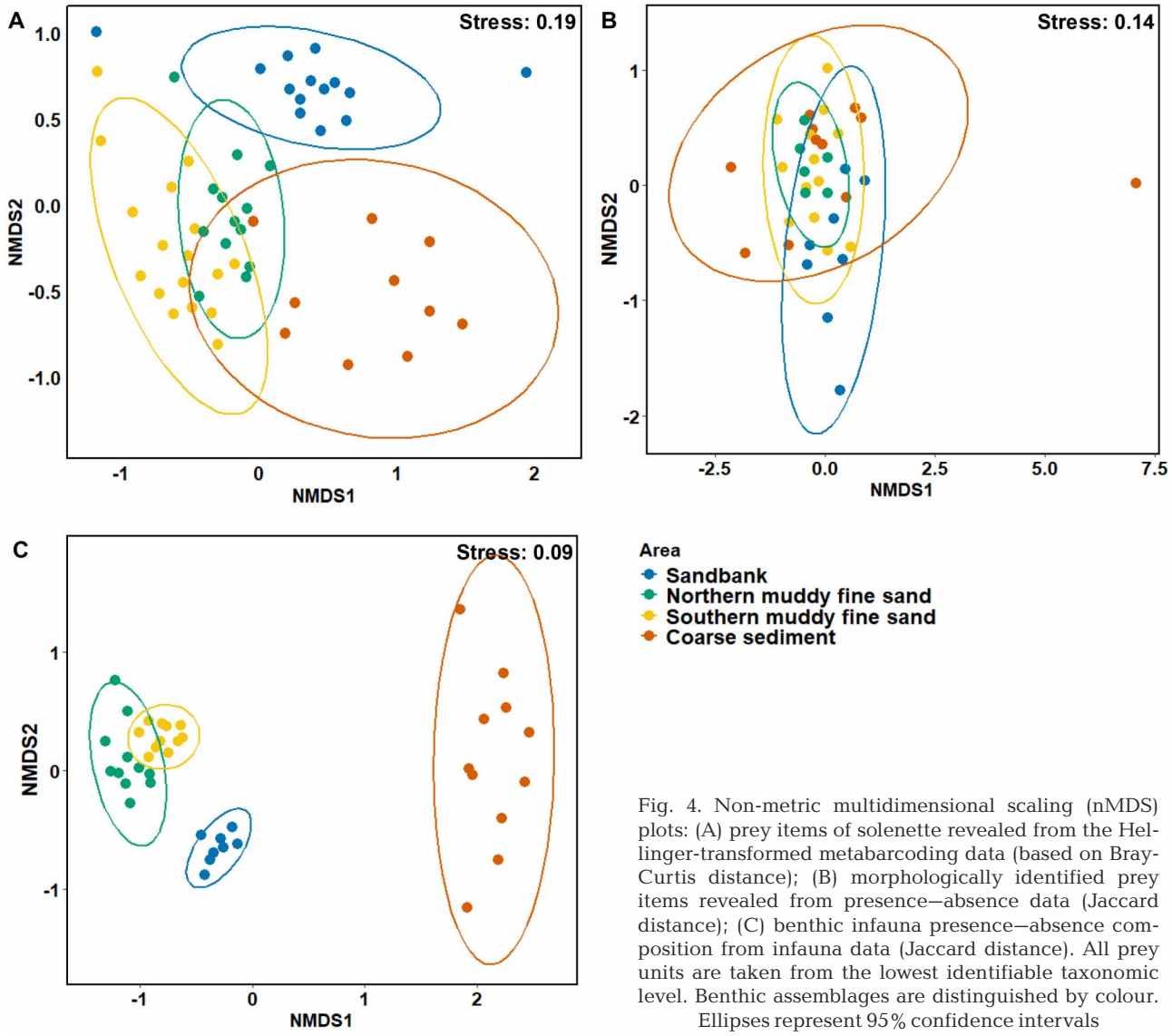

Fig. 4. Non-metric multidimensional scaling (nMDS) plots: (A) prey items of solenette revealed from the Hellinger-transformed metabarcoding data (based on Bray-Curtis distance); (B) morphologically identified prey items revealed from presence–absence data (Jaccard distance); (C) benthic infauna presence–absence composition from infauna data (Jaccard distance). All prey units are taken from the lowest identifiable taxonomic level. Benthic assemblages are distinguished by colour. Ellipses represent 95% confidence intervals

Phyllodocidae, but dominated the diets from the southern muddy fine-sand assemblage (Table 2; 100%). The coarse sediment assemblage stomach content was likewise dominated by *Polybius* (27.2%; Table 2), whereas bivalves were completely absent from fish stomachs collected in this assemblage.

Amphipod prey occurred across all benthic assemblages but were particularly prominent in the sandbank assemblage, which exhibited the highest amphipod diversity (9 families, Table 2). Here, *Bathyporeia* spp. comprised 87.50% of prey (Table 2). Similarly, copepods were ubiquitous across benthic assemblages, especially members of the genus *Pseudobradya* (Table 2).

Ordination showed no clear clustering for diet (Fig. 4B), with the exception of 2 fish from the coarse sediment assemblage that only had 1 identifiable prey item in their stomach. In both cases, the prey item was an oedicerotid amphipod. PERMANOVA indicated no significant differences among benthic assemblages (Table S12; PERMANOVA; pseudo-$F_{3,34}$ = 1.18, p = 0.185). Moreover, plastic threads resembling nylon fishing line were present in 76% of stomachs.

3.4. Prey selection and overlap with infauna

Solenette from the sandbank demonstrated high dietary selectivity for amphipod prey (E = 0.79–0.95; Table 1), reflecting the dominance of amphipods in the local infauna. The only negative electivity value recorded was for the polychaete *Spiophanes bombyx*

Table 2. Morphologically identified prey taxa in stomachs of *Buglossidium luteum* for each benthic assemblage. The frequency of occurrence metric (%FOO) metric is displayed, calculated from the total number of fish stomachs within each assemblage. Many prey items were classified to a lower taxonomic level; however, for the purposes of being ecologically succinct, prey is grouped and %FOO is calculated at the taxonomic level of 'Family'. As a descriptive measure, any prey units belonging to lower taxonomic levels identified from the morphological analysis are listed below each family grouping. The 4 values in **bold** represent the highest prey group noted from morphological analysis within each benthic assemblage

Prey Class	Family	Sandbank (n = 8)	Northern muddy fine sand (n = 6)	Southern muddy fine sand (n = 6)	Coarse sediment (n = 11)
Bivalvia				15.38	
	Cardiidae	37.50	50.00	53.85	
	Acanthocardia				
	Lasaeidae			7.69	
	Tellimya				
	Mactridae		16.67	46.15	
	Spisula				
	Lutraria				
	Nuculidae		16.67	7.69	
	Ennucula				
	Nucula				
	Pharidae	25.00	16.67	15.38	
	Ensis				
	Phaxas				
	Semelidae			15.38	
	Abra				
	Tellinidae			7.69	
	Fabulina				
	Veneridae	12.50	50.00	23.08	
	Chamelea				
Copepoda		25.00	83.33	53.85	45.45
	Ectinosomatidae	12.50	16.67	15.38	18.18
	Pseudobradya				
	Longipediidae			23.08	9.09
	Longipedia				
Echinoidea	Echinidae		33.33		
Gastropoda				15.38	
	Cylichnidae	37.50	33.33	23.08	9.09
	Cylichna				
	Naticidae	25.00	33.33	7.69	
	Euspira				
	Philinidae		16.67		
	Hermania				
	Pyramidellidae				9.09
	Brachystomia				
	Retusidae	12.50	16.67		9.09
	Retusa				
Malacostraca		62.50	50	53.85	**54.55**
	Alpheidae		16.67		
	Crangon				
	Ampeliscidae	12.50			
	Aoridae	25.00			9.09
	Aora				
	Argissidae	37.50			
	Argissa				
	Atylidae	37.50			18.18
	Nototropis				
	Bathyporeiidae	**87.50**		7.69	18.18
	Bathyporeia				
	Bodotriidae	25.00			
	Caprellidae		16.67		
	Phtisica				

Table continued on next page

Table 2 (continued)

Prey Class	Family	Sandbank (n = 8)	Northern muddy fine sand (n = 6)	Southern muddy fine sand (n = 6)	Coarse sediment (n = 11)
	Corystidae		50.00		
	Corystes				
	Crangonidae				45.45
	Diastylidae			7.69	
	Diastylis				
	Ischyroceridae	12.50			
	Centraloecetes				
	Leucothoidae	25.00		7.69	
	Leucothoe				
	Megaluropidae	12.50			
	Megaluropus				
	Microprotopidae	50.00			
	Microprotopus				
	Mysidae				9.09
	Oedicerotidae	50.00	16.67	30.77	27.27
	Perioculodes				
	Pontocrates				
	Synchelidium				
	Paguridae		16.67		
	Pagurus				
	Polybiidae		66.67	**69.24**	27.27
	Polybius				
	Processidae	25.00		15.38	
	Pseudocumatidae	12.50	16.67	15.38	18.18
	Pseudocuma				
	Upogebiidae		16.67		
	Upogebia				
Ophiuroidea				7.69	
	Amphiuridae		16.67		9.09
	Amphiura				
Polychaeta		37.50	**100**	53.85	45.45
	Phyllodocidae			15.38	9.09
	Phyllodoce				
	Spionidae		16.67		
	Spio				

(−0.76; Table 1), indicating avoidance or inaccessibility despite its high field abundance. On muddy fine-sand and coarse sediment assemblages, consistently high electivity values for swimming crabs (*Polybius* spp.) demonstrated strong and repeated selection across these benthic habitats. The mysid *Gastrosaccus spinifer* was also abundant in the infauna of the coarse sediment assemblage, but it was only marginally selected for in the diet (Table 1). Other prey taxa that were both dominant in the local infauna and were strongly selected by the solenette included polychaetes such as *L. conchilega* and *Spio* spp., as well as crustaceans such as *C. crangon, Pilocheras* sp., and *Diastylis laevis* (Table 1).

In general, there was considerable overlap between prey items found in solenette stomachs and taxa present in the corresponding infaunal assemblages. This overlap was greatest in the southern muddy fine-sand assemblage, where 40 prey items were shared between solenette diet and local infauna. Similarly, the amphipod-dominated diet of solenette from the sandbank also largely reflected the local infauna, except for the amphipod *Microprotopus maculatus*, which was only detected in the stomachs. The least diet—infauna overlap occurred in the coarse sediment assemblage, with 17 shared taxa. Here, polychaetes of the genus *Eumida* (*E. bahusiensis*, *E. mackiei*, *E. schanderi*), were even absent from infaunal samples, despite being common, or even dominant (*E. mackiei,* Table 1) in the diet of solenette. Interestingly, the lancet fish *Branchiostoma* was found in fish diets from the southern muddy fine-sand and coarse sediment assemblages, yet only in infauna data from the coarse sediment assemblage.

Prey items present in the diet but absent from infauna samples were predominantly small, fragile soft-bodied polychaetes (e.g. *Gyptis*, *Eumida*), meiofaunal groups, or highly mobile taxa such as the flatfish *L. limanda*.

4. DISCUSSION

4.1. Broad diet revealed through complementary methods

In general, the prey spectra obtained from the 2 methodological approaches were well aligned. However, DNA metabarcoding yielded a broader taxonomic coverage, consistent with previous studies that highlighted a broader taxonomic and higher resolution of DNA metabarcoding (Berry et al. 2015, Granquist et al. 2018, Underwood et al. 2023). Overall, DNA metabarcoding identified prey collected from the stomachs of solenette at lower taxonomic levels, yielding a higher dietary diversity (Fig. 5A; 124 taxa) compared to the dietary diversity determined with only morphological identification (Fig. 5A; 64 taxa). Within the Bivalvia, however, Cardiidae could be identified using metabarcoding only at the family level, whereas 2 cardiid genera (*Acanthocardia* and *Fabulina*) could be distinguished morphologically. Mismatches between metabarcoding and visual analyses have been reported for some taxa such as fish (Granquist et al. 2018) and echinoderms (Cordone et al. 2022). As both bivalve genera were well represented in the utilized reference sequence database, the observed mismatch was likely due to unequal DNA amplification during PCR, where primer amplification biases can occur with certain taxa (Wangensteen et al. 2018, Albaina et al. 2024). While DNA metabarcoding proved to be a powerful tool for species detection, it is inherently semi-quantitative due to amplification bias and dependence on the completeness of reference libraries (Harms-Tuohy et al. 2016, Deagle et al. 2019, Sousa et al. 2019). Further limitations of this method relate to its inability to detect secondary predation or to account for differential digestion rates among prey taxa (Harms-Tuohy et al. 2016, Dick et al. 2023).

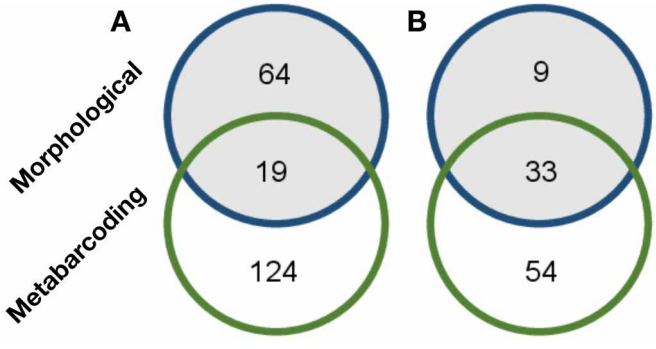

Fig. 5. Overlap of prey units found between the morphological analysis and DNA metabarcoding analysis at (A) the lowest taxonomic identification possible and (B) the broader taxonomic level of Family

Morphological identification proved particularly effective for detecting hard-bodied prey, such as decapod crabs of the genus *Polybius*, complementing the higher taxonomic resolution of metabarcoding. In contrast, soft-bodied prey such as polychaetes posed challenges due to their fragile structures (Amundsen & Sánchez-Hernández 2019), where metabarcoding successfully identified dominant reads from Spionidae and Phyllodocidae. Additionally, benthic feeders like *Buglossidium luteum* often ingest sediment grains, complicating morphological analysis due to a mechanical breakdown of prey. Although fewer stomachs were analysed using the morphological method, the resulting prey patterns were highly consistent across approaches. Any potential effect of differing sample sizes is likely minimal, as similar prey compositions were observed across benthic assemblages in both data sets. Nevertheless, our findings underline the strengths of morphological analysis for certain prey types as well as the benefits of using it as a complementary method to DNA metabarcoding.

The incorporation of infauna data from the same sampling stations to the metabarcoding of stomach contents provides a more comprehensive ecological perspective. To our knowledge, this study is the first to directly compare bulk diet metabarcoding with benthic infaunal data sets in this manner. Here, the congruency between metabarcoding and infaunal data was evident across taxonomic groups. For example, the mysid *G. spinifer* and the polychaete *E. mackei* were dominant in both fish stomachs and grab samples collected from the coarse sediment assemblage. Discrepancies between diet and infauna likely reflect differences in detectability and sampling efficiency between DNA-based stomach analysis and grab-sampled macrofauna rather than true differences in feeding selectivity.

4.2. Differentiated diet of solenette across habitats

The diet of solenette collected in the south-eastern North Sea encompassed a wide range of taxa, with prey composition varying by benthic assemblage. These differences appear largely driven by benthic

species characteristics of each assemblage, as evidenced by their concurrent presence in both infauna samples and solenette stomachs. Amphipod dominance and diversity was particularly pronounced in diets from the sandbank assemblage, reflecting the prevalence of *Bathyporeia* species typical of these sandy environments (Beermann et al. 2023). Although the feeding behaviour of solenette has thus far been undocumented, related Soleidae are known to rely primarily on olfactory senses rather than visual cues when foraging (de Groot 1969, Piet 1998). The close correspondence between diet composition and infaunal assemblages therefore suggests limited mobility in *B. luteum*. If individuals exhibited greater movement between the benthic assemblages, a more homogenized diet reflecting mixed prey from multiple areas would be expected. This is especially evident with respect to the coarse sediment stations, as they are characterized by highly localized patches (<1 km) of distinct sediment types and associated fauna (Gutow et al. 2022). The clear dietary distinctions observed between these assemblages further supports the inference of limited spatial movement in this species and highlight the strong influence of local benthic assemblage structure on the diet of *B. luteum* in the German Bight.

Interestingly, *B. luteum* exhibited notably low dietary diversity in the sandbank assemblage even though this assemblage hosted the highest infaunal diversity among all surveyed areas. The strong dominance of amphipod prey, coupled with visibly satiated stomachs, suggests that the fish obtained sufficient nourishment from these abundant resources, particularly *Bathyporeia* spp. Therefore, individuals may have selectively targeted this energetically favourable resource rather than foraging opportunistically. Such patterns indicate that solenette may switch from opportunistic feeding to more selective foraging when prey availability is exceptionally high (Khait et al. 2013, Gauzens et al. 2024).

In contrast, solenette collected from the muddy fine-sand assemblages exhibited the most diverse diets, dominated by crustacean prey. Surprisingly, other demersal fish such as *Limanda limanda* and *Callionymus lyra* were also detected as prey items in the muddy fine-sand assemblages. This prey occurrence of demersal fish likely represents ingestion of either larval or juvenile stages of these fish, consistent with reported spawning periods (King et al. 1994) and high egg densities of these species in the area (Bils et al. 2012).

Some prey groups were common across the sampled areas, notably harpacticoid copepods, which have been widely reported in solenette diets (Amara et al. 2004, Schückel et al. 2013). In our survey, Longipediidae, particularly *Longipedia* spp., were the most prevalent. Their broad distribution in the North Sea and occurrence in upper sediment layers (Witte & Zijlstra 1984, Huys et al. 1992) makes them easily available benthic prey for solenette, especially as some harpacticoid copepods can occur in very high densities in the southern North Sea (Huys et al. 1992). Furthermore, although the nMDS plot for the morphological stomach data displayed considerable overlap between benthic assemblages, PERMANOVA still revealed significant compositional differences. The limited taxonomic resolution and smaller sample size of the morphological data set, along with variation in prey digestion stage, likely contributed to the reduced visual separation despite underlying differences in diet composition. However, this apparent inconsistency is not unexpected, as PERMANOVA detects differences in overall community composition that may not be clearly visible in a 2-dimensional nMDS plot (Anderson 2001).

Polychaetes represented a consistent component of solenette diet across all benthic assemblages. Specifically, *Lanice conchilega* and *Spio* spp. were abundant in diets from coarse sediments, whereas *Spiophanes bombyx* was more characteristic of the sandbank assemblage. Although *L. conchilega* and *S. bombyx* have been previously reported as prey items of solenette (Nottage & Perkins 1983, Schückel et al. 2011, 2013), polychaetes had not been considered as particularly important prey (Amara et al. 2004, Schückel et al. 2011). The comparatively higher importance of polychaetes in the present study likely reflects improved detection of soft-bodied taxa by DNA metabarcoding, suggesting that earlier morphology-based assessments may have underestimated their role in the diet of this small flatfish.

Nearly all of the top prey items detected through metabarcoding exhibited high selectivity values from the infaunal field data, as indicated by the calculated Ivlev's electivity index. This suggests that *B. luteum* readily consumed for the most part locally abundant prey, highlighting the utility of the index in quantifying prey use relative to availability. However, the uniformly high selectivity across multiple prey taxa likely indicates flexible, opportunistic feeding behaviour rather than strong preference for specific prey types. Although Ivlev's selection values typically indicate prey selection, such uniformly positive values across many prey taxa are not necessarily evidence of strong prey preference. Rather, they can reflect the relative accessibility and abundance of prey in the environ-

ment. In this context, *B. luteum* can be described as opportunistic at the community level — it is able to exploit a broad spectrum of benthic prey, while being selective at the prey-item level, with higher consumption of prey that are both abundant and readily available. This emphasizes that the index expresses relative selectivity and accessibility rather than absolute preference, and should therefore be interpreted in combination with ecological knowledge of prey availability and predator traits. For instance, predator traits such as gape size are primary drivers of prey selection in demersal fishes, as species are also physically limited to prey they can ingest (Ludwig et al. 2024). This is exemplified by the polychaete *S. bombyx,* which showed negative selection. However, *S. bombyx* is a well-represented dietary component of many benthivorous fish (Schückel et al. 2011, 2024), including solenette. Its prevalence as prey despite negative selection could be caused by its continuous abundance throughout many different habitats in the German Bight (Robert et al. 2021, Beermann et al. 2023). On the other hand, the tube-building activity of this polychaete probably represents a physical defence mechanism against predation, although stationery tube builders have been proposed as easier prey than mobile taxa (Nottage & Perkins 1983). Nevertheless, *B. luteum* may also have simply exhibited selective feeding toward energetically valuable crustacean prey, which could explain the clear dominance of crustaceans in its diet as revealed by both DNA metabarcoding and traditional morphological analysis.

To our knowledge, our study is the first to record the lancet fish *Branchiostoma lanceolatum* as solenette prey. This observation was made in stomachs collected from the coarse sediment assemblages but also from the muddy fine sand. Although *B. lanceolatum* is a characteristic species for medium to coarse sands in the North Sea (Gutow et al. 2022), its role as a prey item remained largely unknown. This finding thus elucidates an important link in marine benthic food webs of the North Sea.

4.3. Opportunistic feeding corroborates successful expansion

The successful expansion of *B. luteum* in northern European seas may be closely linked to its highly opportunistic feeding behaviour. Solenette abundances in the North Sea have risen significantly since the 1980s (Jennings et al. 2008, Tulp et al. 2008). This trend is likely sustained by milder winters and warming sea temperatures (van Hal et al. 2010, Amorim et al. 2023). The population increase must be regarded in a broader ecological context; across various global ecosystems, the reduction of larger predatory fish has been linked to an increase in populations of smaller predatory fish, a process referred to as 'mesopredator release' (Baum & Worm 2009, Ritchie & Johnson 2009, Eriksson et al. 2011). A well-known example is the collapse of the North Atlantic cod fishery, which facilitated the expansion of medium-sized predators like herring *Clupea harengus* and sand lance *Ammodytes dubius* (Baum & Worm 2009).

Our findings suggest that *B. luteum* may similarly benefit from such ecosystem shifts. Its ability to exploit a wide range of previously undocumented dietary items, including *Bathyporeia* spp. and *Spio* spp. across various benthic communities, highlights a dietary flexibility that could facilitate its continued success. However, while our results characterize the diet in high resolution, the extent to which mesopredator release or competitive interactions are currently driving these trends remains a subject for further empirical investigation.

An increase in solenette abundance could thus theoretically lead to increased competition for food resources with other demersal fish species such as dab *Limanda limanda*, hooknose *Agonus cataphractus*, plaice *Pleuronectes platessa*, and scaldfish *Arnoglossus laterna* (Rijnsdorp et al. 1992, Amara et al. 2001, De Raedemaecker et al. 2011, Paulo-Martins et al. 2011, Schückel et al. 2012, 2024), which share overlapping prey spectra. No direct indication for resource competition was found within the scope of this study, and existing literature suggests that seasonal partitioning may mitigate these effects (Schoener 1986, Schückel et al. 2013). However, the rising abundance of opportunistic mesopredators warrants attention, as many of these commercially unimportant species still increase in abundance (van Hal et al. 2010, Fock et al. 2014). Given its ability to exploit a range of benthic 'ecosystem engineers' such as the bioirrigating tubeworm species *L. conchilega* and bioturbators such as the sea potato *Echinocardium cordatum* (Braeckman et al. 2014, Wrede et al. 2017), solenette may have cascading effects on biogeochemical pathways and ecosystem functioning. Our results provide the necessary baseline for such studies, identifying the specific taxa that would be most affected.

5. CONCLUSION

The DNA metabarcoding of stomach contents is an efficient method for diet assessments of fish, that can

be complemented by morphological analyses. Such molecular approaches are particularly valuable, as trophic data will become essential for the successful implementation of ecosystem-based management frameworks (Canals et al. 2024). However, the direct correlation of individual diets with infaunal data from corresponding habitats is needed in order to elucidate the ecological complexity of trophic relationships, providing crucial information on predator mobility and prey selectivity. Furthermore, food web studies often rely on data obtained from commercially targeted species, potentially omitting substantial elements of marine benthic food webs. In the light of shifts in species' geographic distributions and biological diversity, as well as intensified anthropogenic use of the oceans (e.g. fishing pressure, offshore constructions), holistic approaches to benthic trophic ecology could improve the detection and prediction of possible implications for marine ecosystems in ongoing environmental change.

Ethics statement. The German animal protection laws do not require permission for the use of fish from net hauls and towed dredges. The fish collected are neither endangered nor protected within the German Bight of the North Sea. This study was carried out with all possible procedures that minimised the pain and suffering of the sampled fish.

Data availability. The raw metabarcoding sequencing data from this project are available at NCBI on the SRA database under the BioProject ID: PRJNA1142860, public upon publication. Morphologically identified stomach content data will be available in the data repository PANGAEA (Felden et al. 2023) upon publication (https://doi.pangaea.de/10.1594/PANGAEA.988899). Infaunal data sets from corresponding stations are stored in Critterbase (critterbase.awi.de; Teschke et al. 2022), and will be made available upon request.

Acknowledgements. We thank Micaela Ruiz for her practical help as well as Charlotte Havermans and Andrea Eschbach of the ARJEL group at the AWI for their support while using their laboratory facilities. We further thank the crew of the RV 'Heincke' for their support during the cruise. J.B. was financially supported by the German Federal Agency for Nature Conservation (grant no. 3519532201, LABEL project). Lastly, we thank the 3 anonymous reviewers for their valuable input.

LITERATURE CITED

Albaina A, Garic R, Yebra L (2024) Know your limits; mini-COI metabarcoding fails with key marine zooplankton taxa. J Plankton Res 46:581–595

Amara R, Laffargue P, Dewarumez JM, Maryniak C, Lagardére F, Luzac C (2001) Feeding ecology and growth of O-group flatfish (sole, dab and plaice) on a nursery ground (Southern Bight of the North Sea). J Fish Biol 58:788–803

Amara R, Mahé K, LePape O, Desroy N (2004) Growth, feeding and distribution of the solenette *Buglossidium luteum* with particular reference to its habitat preference. J Sea Res 51:211–217

Amundsen PA, Sánchez-Hernández J (2019) Feeding studies take guts — critical review and recommendations of methods for stomach contents analysis in fish. J Fish Biol 95:1364–1373

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Andrews S (2010) FastQC: a quality control tool for high throughput sequence data. Babraham Bioinformatics. https://www.bioinformatics.babraham.ac.uk/projects/fastqc/

Andújar C, Arribas P, Yu DW, Vogler AP, Emerson BC (2018) Why the COI barcode should be the community DNA metabarcode for the metazoa. Mol Ecol 27:3968–3975

Antich A, Palacin C, Wangensteen OS, Turon X (2021) To denoise or to cluster, that is not the question: optimizing pipelines for COI metabarcoding and metaphylogeography. BMC Bioinformatics 22:177

Baker R, Buckland A, Sheaves M (2014) Fish gut content analysis: robust measures of diet composition. Fish Fish 15:170–177

Baltus CAM, Van der Veer HW (1995) Nursery areas of solenette *Buglossidium luteum* (Risso, 1810) and scaldfish *Arnoglossus laterna* (Walbaum, 1792) in the southern North Sea. Neth J Sea Res 34:81–87

Barco A, Raupach MJ, Laakmann S, Neumann H, Knebelsberger T (2016) Identification of North Sea molluscs with DNA barcoding. Mol Ecol Resour 16:288–297

Barco A, Kullmann B, Knebelsberger T, Sarrazin V and others (2022) Detection of fish species from marine protected areas of the North Sea using environmental DNA. J Fish Biol 101:722–727

Barnett DJM, Arts ICW, Penders J (2021) microViz: an R package for microbiome data visualization and statistics. J Open Source Softw 6:3201

Barrera-Oro E, Moreira E, Seefeldt MA, Valli Francione M, Quartino ML (2019) The importance of macroalgae and associated amphipods in the selective benthic feeding of sister rockcod species *Notothenia rossii* and *N. coriiceps* (Nototheniidae) in West Antarctica. Polar Biol 42:317–334

Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. J Anim Ecol 78: 699–714

Beermann J, Gutow L, Wührdemann S, Konijnenberg R and others (2023) Characterization and differentiation of sublittoral sandbanks in the southeastern North Sea. Int J Biodivers Conserv 32:2747–2768

Berry O, Bulman C, Bunce M, Coghlan M, Murray DC, Ward RD (2015) Comparison of morphological and DNA metabarcoding analyses of diets in exploited marine fishes. Mar Ecol Prog Ser 540:167–181

Bils F, Kanstinger P, Kloppman MHF, Peck MA (2012) Habitat partitioning by fish larvae among coastal, offshore, and frontal zones in the southern North Sea. Aquat Biol 15:237–250

Braeckman U, Rabaut M, Vanaverbeke J, Degraer S, Vincx M (2014) Protecting the commons: the use of subtidal ecosystem engineers in marine management. Aquat Conserv 24:275–286

Buchner D, Leese F (2020) BOLDigger — a Python package to identify and organise sequences with the Barcode of Life Data systems. Metabarcoding Metagenomics 4:53535

Buchner D, Macher TH, Leese F (2022) APSCALE: advanced pipeline for simple yet comprehensive analyses of DNA metabarcoding data. Bioinformatics 38:4817–4819

Canals O, Lanzén A, Mendibil I, Bachiller E and others (2024) Increasing marine trophic web knowledge through DNA analyses of fish stomach content: a step towards an ecosystem-based approach to fisheries research. J Fish Biol 105:431–443

Cordone G, Lozada M, Vilacoba E, Thalinger B and others (2022) Metabarcoding, direct stomach observation and stable isotope analysis reveal a highly diverse diet for the invasive green crab in Atlantic Patagonia. Biol Invasions 24:505–526

Davies C, Moss D, Hill MO (2004) EUNIS habitat classification. European Environment Agency European Topic Centre on Nature Protection and Biodiversity. https://eunis.eea.europa.eu/habitats.jsp

de Amorim FLL, Wiltshire KH, Lemke P, Carstens K and others (2023) Investigation of marine temperature changes across temporal and spatial gradients: providing a fundament for studies on the effects of warming on marine ecosystem function and biodiversity. Prog Oceanogr 216:103080

de Groot SJ (1969) Digestive system and sensorial factors in relation to the feeding behaviour of flatfish (Pleuronectiformes). ICES J Mar Sci 32:385–394

De Raedemaecker F, O'Connor I, Brophy D, Black A (2011) Macrobenthic prey availability and the potential for food competition between 0 year group *Pleuronectes platessa* and *Limanda limanda.* J Fish Biol 79:1918–1939

Deagle BE, Thomas AC, McInnes JC, Clarke LJ and others (2019) Counting with DNA in metabarcoding studies: How should we convert sequence reads to dietary data? Mol Ecol 28:391–406

Derycke S, Maes S, Van den Bulcke L, Vanhollebeke J and others (2021) Detection of macrobenthos species with metabarcoding is consistent in bulk DNA but dependent on body size and sclerotization in eDNA from the ethanol preservative. Front Mar Sci 8:637858

Dick C, Larson WA, Karpan K, Baetscher DS and others (2023) Prey ration, temperature, and predator species influence digestion rates of prey DNA inferred from qPCR and metabarcoding. Mol Ecol Resour 25:e13849

Diesing M, Kubicki A, Winter C, Schwarzer K (2006) Decadal scale stability of sorted bedforms, German Bight, southeastern North Sea. Cont Shelf Res 26:902–916

Dischereit A, Beermann J, Lebreton B, Wangensteen OS, Neuhaus S, Havermans C (2024a) DNA metabarcoding reveals a diverse, omnivorous diet of Arctic amphipods during the polar night, with jellyfish and fish as major prey. Front Mar Sci 11:1327650

Dischereit A, Throm JK, Werner KM, Neuhaus S, Havermans C (2024b) A belly full of jelly? DNA metabarcoding shows evidence for gelatinous zooplankton predation by several fish species in Greenland waters. R Soc Open Sci 11:240797

Drake LE, Cuff JP, Young RE, Marchbank A, Chadwick EA, Symondson WOC (2022) An assessment of minimum sequence copy thresholds for identifying and reducing the prevalence of artefacts in dietary metabarcoding data. Methods Ecol Evol 13:694–710

Ducrotoy JP, Elliott M, de Jonge VN (2000) The North Sea. Mar Pollut Bull 41:5–23

Dunn OJ (1961) Multiple comparisons among means. J Am Stat Assoc 56:52–64

Edgar RC (2010) Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26:2460–2461

Eggleton JD, Depestele J, Kenny AJ, Bolam SG, Garcia C (2018) How benthic habitats and bottom trawling affect trait composition in the diet of seven demersal and benthivorous fish species in the North Sea. J Sea Res 142: 132–146

Ehrich S, Weber W, Zimmermann C (1998) A four-week area closure in the German Bight: a measure to protect the strong 1996 cod year-class. ICES, Copenhagen

Ellis JR, Maxwell T, Schratzberger M, Rogers SI (2011) The benthos and fish of offshore sandbank habitats in the southern North Sea. J Mar Biol Assoc UK 91:1319–1335

Emery AR, Hodgson DM, Barlow NLM, Carrivick JL, Cotterill CJ, Mellett CL, Booth AD (2019) Topographic and hydrodynamic controls on barrier retreat and preservation: an example from Dogger Bank, North Sea. Mar Geol 416:105981

Eriksson BK, Sieben K, Eklöf J, Ljunggren L, Olsson J, Casini M, Bergström U (2011) Effects of altered offshore food webs on coastal ecosystems emphasize the need for cross-ecosystem management. Ambio 40:786–797

Ershova EA, Wangensteen OS, Falkenhaug T (2023) Mock samples resolve biases in diversity estimates and quantitative interpretation of zooplankton metabarcoding data. Mar Biodivers 53:66

Felden J, Möller L, Schindler U, Huber R and others (2023) PANGAEA — data publisher for earth & environmental science. Sci Data 10:347

Fock HO, Kloppmann MHF, Probst WN (2014) An early footprint of fisheries: changes for a demersal fish assemblage in the German Bight from 1902–1932 to 1991–2009. J Sea Res 85:325–335

Fox CJ, Weisberg S (2019) An R companion to applied regression. Sage, Thousand Oaks, CA

Frøslev TG, Kjøller R, Bruun HH, Ejrnaes R, Brunbjerg AK, Pietroni C, Hansen AJ (2017) Algorithm for post-clustering curation of DNA amplicon data yields reliable biodiversity estimates. Nat Commun 8:1188

Gao CH, Chen C, Akyol T, Dusa A, Yu G, Cao B, Cai P (2024) ggVennDiagram: intuitive Venn diagram. iMeta 3:e177

Gauzens B, Rosenbaum B, Kalinkat G, Boy T and others (2024) Flexible foraging behaviour increases predator vulnerability to climate change. Nat Clim Change 14: 387–392

Granquist SM, Esparza-Salas R, Hauksson E, Karlsson O, Angerbjörn A (2018) Fish consumption of harbour seals (*Phoca vitulina*) in north western Iceland assessed by DNA metabarcoding and morphological analysis. Polar Biol 41:2199–2210

Günther B, Fromentin JM, Metral L, Arnaud-Haond S (2021) Metabarcoding confirms the opportunistic foraging behaviour of Atlantic bluefin tuna and reveals the importance of gelatinous prey. PeerJ 9:e11757

Gutow L, Günther CP, Ebbe B, Schückel S and others (2020) Structure and distribution of a threatened muddy biotope in the south-eastern North Sea. J Environ Manage 255: 109876

Gutow L, Gusky M, Beermann J, Gimenez L and others (2022) Spotlight on coarse sediments: comparative characterization of a poorly investigated seafloor biotope in the German Bight (SE North Sea). Estuar Coast Shelf Sci 275:107996

Harms-Tuohy CA, Schizas NV, Appeldoorn RS (2016) Use of DNA metabarcoding for stomach content analysis in the

invasive lionfish *Pterois volitans* in Puerto Rico. Mar Ecol Prog Ser 558:181–191
Heessen HJL, Daan N (1996) Long term trends in ten non-target North Sea fish species. ICES J Mar Sci 53: 1063–1078
Heindler FM, Maes GE, Delerue-Ricard S, Vanden Bavière A, Hostens K, Volckaert FAM (2019) Diet composition and gut microbiome of 0-group European plaice *Pleuronectes platessa* L. — strong homogeneity and subtle spatial and temporal differences. J Sea Res 144:67–77
Hiddink JG, Moranta J, Balestrini S, Sciberras M and others (2016) Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors. J Appl Ecol 53:1500–1510
Hjermann DØ, Fisher JAD, Rouyer T, Frank KT, Stenseth NC (2013) Spatial analysis of North Sea cod recruitment: concurrent effects of changes in spawning stock biomass, temperature and herring abundance. Mar Ecol Prog Ser 480:263–275
Huys R, Herman PMJ, Heip CHR, Soetaert K (1992) The meiobenthos of the North Sea: density, biomass trends and distribution of copepod communities. ICES J Mar Sci 49:23–44
Ivlev VS (1962) Experimental ecology of the feeding of fishes, Vol 1. Yale University Press, New Haven, CT
Jacobs J (1974) Quantitative measure of food selection. Oecologia 14:413–417
Jennings S, Pinnegar JK, Polunin NVC, Warr KJ (2001) Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. Mar Ecol Prog Ser 213:127–142
Jennings S, van Hal R, Hiddink JG, Maxwell TAD (2008) Fishing effects on energy use by North Sea fishes. J Sea Res 60:74–88
Jiming Y (1982) The dominant fish fauna in the North Sea and its determination. J Fish Biol 20:635–643
Khait R, Obolski U, Hadany L, Genin A (2013) Food selectivity and diet switch can explain the slow feeding of herbivorous coral-reef fishes during the morning. PLOS ONE 8:e82391
King PA, Fives JM, McGrath D (1994) Reproduction, growth and feeding of the dragonet, *Callionymus lyra* (Teleostei: Callionymidae), in Galway Bay, Ireland. J Mar Biol Assoc UK 74:513–526
Kröncke I, Reiss H, Eggleton JD, Aldridge J and others (2011) Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. Estuar Coast Shelf Sci 94:1–15
Künitzer A, Basford D, Craeymeersch JA, Dewarumez JM and others (1992) The benthic infauna of the North Sea: species distribution and assemblages. ICES J Mar Sci 49: 127–143
Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280
Leray M, Knowlton N (2015) DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity. Proc Natl Acad Sci USA 112:2076–2081
Leray M, Yang JY, Meyer CP, Mills SC and others (2013) A new versatile primer set targeting a short fragment of the mitochondrial COI region for metabarcoding metazoan diversity: application for characterizing coral reef fish gut contents. Front Zool 10:34
Ludwig KE, Singer A, Kröncke I, Sell AF (2024) Predator–prey trait associations and feeding preferences of demersal fishes in the southern North Sea. Mar Ecol Prog Ser 739:173–190
Martin M (2011) Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet J 17:10–12
Martinez Arbizu P (2020) pairwiseAdonis: Pairwise multilevel comparison using adonis. https://github.com/pmartinezarbizu/pairwiseAdonis
Mauffrey F, Cordier T, Apotheloz-Perret-Gentil L, Cermakova K and others (2021) Benthic monitoring of oil and gas offshore platforms in the North Sea using environmental DNA metabarcoding. Mol Ecol 30:3007–3022
McMurdie PJ, Holmes S (2013) phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. PLOS ONE 8:e61217
Möllmann C, Folke C, Edwards M, Conversi A (2015) Marine regime shifts around the globe: theory, drivers and impacts. Philos Trans R Soc B 370:20130260
Murray A, Priest T, Antich A, von Appen WJ, Neuhaus S, Havermans C (2024) Investigating pelagic biodiversity and gelatinous zooplankton communities in the rapidly changing European Arctic: an eDNA metabarcoding survey. Environ DNA 6:e569
Neumann A, van Beusekom JEE, Eisele A, Emeis KC and others (2021) Macrofauna as a major driver of benthopelagic exchange in the southern North Sea. Limnol Oceanogr 66:2203–2217
Nottage AS, Perkins EJ (1983) The biology of solenette, *Buglossidium luteum* (Risso), in the Solway Firth. J Fish Biol 22:21–27
Novotny A, Jan KMG, Dierking J, Winder M (2022) Niche partitioning between planktivorous fish in the pelagic Baltic Sea assessed by DNA metabarcoding, qPCR and microscopy. Sci Rep 12:10952
Oksanen J, Kindt R, Legendre P, O'Hara B and others (2022) vegan: Community ecology package. R package version 2.6-4. https://cran.r-project.org/package=vegan
Paliy O, Shankar V (2016) Application of multivariate statistical techniques in microbial ecology. Mol Ecol 25: 1032–1057
Paulo-Martins C, Vinagre C, Silva A, Cabral H (2011) Variation of diet and food consumption of the scaldfish *Arnoglossus laterna* (Walbaum, 1792). J Appl Ichthyol 27: 977–983
Piet GJ, Pfisterer AB, Rijnsdorp AD (1998) On factors structuring the flatfish assemblage in the southern North Sea. J Sea Res 40:143–152
Piñol J, San Andrés V, Clare EL, Mir G, Symondson WOC (2014) A pragmatic approach to the analysis of diets of generalist predators: the use of next-generation sequencing with no blocking probes. Mol Ecol Resour 14:18–26
R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Ralser M, Querfurth R, Warnatz HJ, Lehrach H, Yaspo ML, Krobitsch S (2006) An efficient and economic enhancer mix for PCR. Biochem Biophys Res Commun 347:747–751
Ratnasingham S, Hebert PD (2007) bold: The Barcode of Life Data System (www.barcodinglife.org). Mol Ecol Notes 7: 355–364
Rijnsdorp AD, Vethaak AD, Van Leeuwen PI (1992) Population biology of dab *Limanda limanda* in the southeastern North Sea. Mar Ecol Prog Ser 91:19–35
Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998

Robert AE, Quillien N, Bacha M, Caulle C and others (2021) Sediment migrations drive the dynamic of macrobenthic ecosystems in subtidal sandy bedforms. Mar Pollut Bull 171:112695

Rognes T, Flouri T, Nichols B, Quince C, Mahe F (2016) VSEARCH: a versatile open source tool for metagenomics. PeerJ 4:e2584

Salzwedel H, Rachor E, Gerdes D (1985) Benthic macrofauna communities in the German Bight. Veröff Inst Meeresforsch Bremerhav 20:199–267

Schaafsma FL, Flores H, David CL, Castellani G and others (2024) Insights into the diet and feeding behavior of immature polar cod (*Boreogadus saida*) from the underice habitat of the central Arctic Ocean. J Fish Biol 105: 907–930

Schoener TW (1986) Resource partitioning. In: Kikkiwa J, Anderson DK (eds) Community ecology: process and patterns. Blackwell Scientific Publications, Melbourne, p 91–126

Schückel S, Sell A, Kröncke I, Reiss H (2011) Diet composition and resource partitioning in two small flatfish species in the German Bight. J Sea Res 66:195–204

Schückel S, Sell AF, Kroncke I, Reiss H (2012) Diet overlap among flatfish species in the southern North Sea. J Fish Biol 80:2571–2594

Schückel S, Sell AF, Kihara TC, Koeppen A, Kröncke I, Reiss H (2013) Meiofauna as food source for small-sized demersal fish in the southern North Sea. Helgol Mar Res 67: 203–218

Schückel S, Rothmeyer J, Jaklin S, Heubel K, Schückel U (2024) Diet composition of the hooknose (*Agonus cataphractus*, L.) in different habitats of coastal waters in the German Wadden Sea (southern North Sea). Mar Biodivers 54:66

Sell AF, Kröncke I (2013) Correlations between benthic habitats and demersal fish assemblages — a case study on the Dogger Bank (North Sea). J Sea Res 80:12–24

Siegenthaler A, Wangensteen OS, Benvenuto C, Campos J, Mariani S (2019) DNA metabarcoding unveils multiscale trophic variation in a widespread coastal opportunist. Mol Ecol 28:232–249

Sonnewald M, Türkay M (2012) The megaepifauna of the Dogger Bank (North Sea): species composition and faunal characteristics 1991–2008. Helgol Mar Res 66: 63–75

Sousa LL, Silva SM, Xavier R (2019) DNA metabarcoding in diet studies: unveiling ecological aspects in aquatic and terrestrial ecosystems. Environ DNA 1:199–214

Stride AH (1959) On the origin of the Dogger Bank, in the North Sea. Geol Mag 96:33–44

Teschke K, Kraan C, Kloss P, Andresen H and others (2022) CRITTERBASE, a science-driven data warehouse for marine biota. Sci Data 9:483

Tiano JC, van der Reijden KJ, O'Flynn S, Beauchard O and others (2020) Experimental bottom trawling finds resilience in large-bodied infauna but vulnerability for epifauna and juveniles in the Frisian Front. Mar Environ Res 159:104964

Tiano JC, De Borger E, O'Flynn S, Cheng CH, van Oevelen D, Soetaert K (2021) Physical and electrical disturbance experiments uncover potential bottom fishing impacts on benthic ecosystem functioning. J Exp Mar Biol Ecol 545: 151628

Traugott M, Thalinger B, Wallinger C, Sint D (2021) Fish as predators and prey: DNA-based assessment of their role in food webs. J Fish Biol 98:367–382

Tulp I, Bolle LJ, Rijnsdorp AD (2008) Signals from the shallows: in search of common patterns in long-term trends in Dutch estuarine and coastal fish. J Sea Res 60:54–73

Underwood LH, van der Reis A, Jeffs AG (2023) Diet of snapper (*Chrysophrys auratus*) in green-lipped mussel farms and adjacent soft-sediment habitats. Aquacult Fish Fish 3:268–286

Van Beusekom JEE, Buschbaum C, Reise K (2012) Wadden Sea tidal basins and the mediating role of the North Sea in ecological processes: scaling up of management? Ocean Coast Manage 68:69–78

van der Reijden KJ, Hintzen NT, Govers LL, Rijnsdorp AD, Olff H (2018) North Sea demersal fisheries prefer specific benthic habitats. PLOS ONE 13:e0208338

van Hal R, Smits K, Rijnsdorp AD (2010) How climate warming impacts the distribution and abundance of two small flatfish species in the North Sea. J Sea Res 64:76–84

van Hal R, van Kooten T, Rijnsdorp AD (2016) Temperature induced changes in size dependent distributions of two boreal and three Lusitanian flatfish species: a comparative study. J Sea Res 107:14–22

Wangensteen OS, Palacin C, Guardiola M, Turon X (2018) DNA metabarcoding of littoral hard-bottom communities: high diversity and database gaps revealed by two molecular markers. PeerJ 6:e4705

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag New York, NY

Witte JIJ, Zijlstra JJ (1984) The meiofauna of a tidal flat in the western part of the Wadden Sea and its role in the benthic ecosystem. Mar Ecol Prog Ser 14:129–138

Wrede A, Dannheim J, Gutow L, Brey T (2017) Who really matters: influence of German Bight key bioturbators on biogeochemical cycling and sediment turnover. J Exp Mar Biol Ecol 488:92–101

Editorial responsibility: Thomas Wernberg, Crawley, Western Australia, Australia
Reviewed by: G. Gül and 2 anonymous referees
Submitted: April 3, 2025; Accepted: February 20, 2026
Proofs received from author(s): May 14, 2026