Predator–prey trait associations and feeding preferences of demersal fishes in the southern North Sea

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ABSTRACT: In marine ecosystems under ongoing long-term changes, reducing complex food webs to their functionally important properties enables systematic analysis of bottom-up/top-down regulations and species turnover. The assessment of feeding interactions in the form of predator and prey trait associations provides a better understanding of predators' criteria for prey selection and thus is a promising approach to reduce complexity. Here, we tested RLQ ordination and fourth-corner analysis, complementary multivariate approaches, as tools to identify ecologically relevant associations between the traits of 8 demersal fish species in the southern North Sea and their fish or benthic prey. To scrutinize the trait-based results in their appropriateness to reflect selective feeding behaviour of the predator species, we compared them with a taxon-based electivity index, Chesson's α. Among 7 predator traits investigated, body tissue composition represented by omega-3 polyunsaturated fatty acid content was significantly associated with prey traits, being positively correlated with energy density of the prey and negatively with prey of low mobility. Comparisons with the electivity indices showed that the prey preferred by predators corresponded relatively well with the identified prey trait preferences. The results of the tested analysis approach support its use when assessing the mutual dependences of predator and prey populations on a functional level. Provided the data availability and quality of feeding-related traits is sufficiently high, trait-based predator—prey analysis with RLQ and fourth-corner analyses offers new possibilities for understanding food web dynamics in the context of climate-change-induced species distribution shifts.

KEY WORDS: Predator—prey interaction · Traits · Cross-taxa · RLQ ordination · Fourth-corner analysis · Chesson's α · Demersal fishes

1. INTRODUCTION

Marine food webs are complex ecological networks characterized by predator—prey interactions between species at different trophic levels (Emmerson 2012). In addition to interspecific interactions, environmental factors (e.g. nutrient levels, atmospheric pressure oscillation) and anthropogenic impacts (e.g. fishing activities, invasive species, climate change) influence the dynamics within food webs, driving bottom-up or top-down regulatory processes (Frank et al. 2007, Lynam et al. 2017). The dynamic and complex nature of food webs poses a challenge to ecologists and marine resource managers when it comes to projecting the future impacts of environmental and anthropogenic pressures on marine organisms and habitats (Benoît & Swain 2008, Llope et al. 2011, Doney et al. 2012). To understand the underlying functional drivers of food-web structures, an appropriate methodological framework is needed.

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A frequently used concept for studying functional aspects of species communities is that of functional traits. The term 'trait' refers to characteristics that are measurable at the level of an individual organism (morphological, behavioural, physiological, or life history properties) and can be compared across species or even communities (McGill et al. 2006). 'Functional traits' are traits which influence an organism's fitness and are therefore under selection pressure, linking them closely to the ecological niches that species occupy within an ecosystem (McGill et al. 2006, Violle et al. 2007). By shifting from taxonomic identities to trait-based descriptions of predators and their prey, this concept can also be used for the functional analysis of predator—prey interactions (e.g. Hinz et al. 2005, Tall et al. 2006, Reecht et al. 2013, Spitz et al. 2014, Gutiérrez-Cánovas et al. 2021).

Three trait groups are particularly useful to describe feeding relationships. Topological traits address the probability of a feeding interaction, relating to morphological or toxicological properties of predator and prey as well as their use of space and time (Gravel et al. 2016). Consumption traits define the frequency of occurrence of predator—prey interactions (e.g. handling time, digestibility), and life history traits delineate predator and prey population dynamics (age at maturity, growth rate) and their mutual dependence (Gravel et al. 2016). Identifying key traits driving feeding interactions between predator and prey species appears to be a promising approach to reducing food web complexity by focusing on functionally meaningful associations.

For the identification of predator—prey trait associations, one framework for biological trait analysis has been suggested as particularly useful (Tall et al. 2006, Spitz et al. 2014, Beauchard et al. 2017), combining 2 methods: fourth-corner analysis (Legendre et al. 1997, Dray & Legendre 2008) and RLQ ordination (Dolédec et al. 1996). Initially developed for the analysis of trait—environment associations, both methods link species traits with environmental variables based on species distributions over sampling sites (Dray & Legendre 2008, Dray et al. 2014). The approach was adopted by some authors to study predator—prey trait associations, linking predator and prey traits based on the prey distributions over predators in a diet matrix (Tall et al. 2006, Spitz et al. 2014). In a study on marine mammal feeding, combining this modified version of the fourth-corner and RLQ analyses with a clustering routine enabled the identification of functionally similar feeding groups, providing new and valuable information for ecosystem management purposes (Spitz et al. 2014).

In the food web of the southern North Sea, demersal fish predators feed on both benthic invertebrates and fishes. Some predators, including commercially important species such as plaice *Pleuronectes platessa* (Bromley et al. 1997, Schückel et al. 2011, 2012, Eggleton et al. 2018), common dab *Limanda limanda* (Bromley et al. 1997, Hinz et al. 2005, Eggleton et al. 2018), and haddock *Melanogrammus aeglefinus* (Schückel et al. 2010, Eggleton et al. 2018), are primarily benthivorous, while others, such as whiting *Merlangius merlangus* (Pedersen 1999, Temming et al. 2004), turbot *Scophthalmus maximus* (Bromley et al. 1997), or greater sandeel *Hyperoplus lanceolatus* (Engelhard et al. 2008), are predominantly or exclusively piscivorous. Generalist species such as Atlantic cod *Gadus morhua* and grey gurnard *Eutrigla gurnardus* feed on a mix of benthic invertebrate and fish prey (e.g. Rindorf et al. 2006, Weinert et al. 2010, Hüssy et al. 2016). Ontogenetic shifts from a more benthivorous diet as juveniles to a piscivorous diet as adults are known to occur in some fishes (e.g. Pedersen 1999, Floeter & Temming 2005, Schückel et al. 2010). Thus, in terms of food web interactions, demersal fish populations are tightly linked to each other as well as to benthic invertebrate communities.

The diet composition of fishes has traditionally been evaluated by analysing the stomach contents of wild-caught specimens (Hyslop 1980, Daan 1989, ICES 1997, Buckland et al. 2017, Amundsen & Sánchez-Hernández 2019). Stomach content analysis provides insights into the prey spectrum and prevalence. Its suitability for the evaluation of actual prey preferences, however, is limited since it constitutes presence data only. In the (typical) absence of data on benthos collected directly in fisheries surveys, some authors have made informative attempts to relate broad-scale species distribution patterns of benthic organisms with the prey items found in fish stomachs (Marchal et al. 2021). However, prey availability in the field is not captured when considering stomach contents only, leaving the question unanswered whether the prey composition found in a stomach is the consequence of active selection or mirrors prey availability in the field. A compelling way of disentangling apparent and actual prey selection is the calculation of electivity indices, comparing relative proportions of prey in the stomach with those in the environment (Lechowicz 1982, Schückel et al. 2010, Amundsen & Sánchez-Hernández 2019). Consideration of the prey available to fishes in the field is particularly important in the light of ongoing long-term changes happening in marine ecosystems, including the southern North Sea.

Global warming has been leading to a particularly strong temperature increase in the southern North Sea (ca. 0.3°C per decade; see Núñez-Riboni & Akimova 2015, Oesterwind et al. 2022) and causes systematic shifts in species distributions and community structure in North Sea fishes and benthic invertebrates (Perry et al. 2005, Dulvy et al. 2008, Rijnsdorp et al. 2009, Hiddink et al. 2015). This development raises the question whether vacant positions in the food web will be filled by species of similar functions. In this context, predator—prey analysis for North Sea fishes and their prey on a purely functional (i.e. trait-based) level is relevant for evaluating the implications of species turnover for the food web. Still, few studies have considered functional links between North Sea demersal fishes and their prey (e.g. Piet et al. 1998, Hinz et al. 2005, Schückel et al. 2010, Eggleton et al. 2018), and a fully trait-based framework of feeding interactions between demersal fishes and their prey has only been applied to Celtic Sea communities so far (Reecht et al. 2013).

Using stomach content data sets assembled from several public and institutional sources, trait information, and field data on abundances of fish and benthic organisms, this study aimed (1) to assess feeding-related trait linkages between demersal North Sea fishes and their prey using the RLQ and fourth-corner analysis framework, testing the applicability of this method to fish—benthos feeding interactions, and (2) to compare the results with information on taxonomic prey composition and preferences. We hypothesized that the trait-based analysis framework is a suitable tool for ordinating predators and prey types based on their functional traits, driven by predators' preferences for certain prey functional properties. By comparing the results to traditional taxonomy-based diet study metrics, we scrutinize our results to achieve a proof of concept.

2. MATERIALS AND METHODS

2.1. Study area

The study area was the shallow southern North Sea down to 50 m depth (Fig. 1). This depth contour is a good proxy for the distinction between northern and southern North Sea communities of benthic invertebrates and demersal fishes, as it constitutes a natural separation line between hydrographical conditions (Callaway et al. 2002, Reiss et al. 2010). The northern North Sea has relatively stable bottom water tempera-
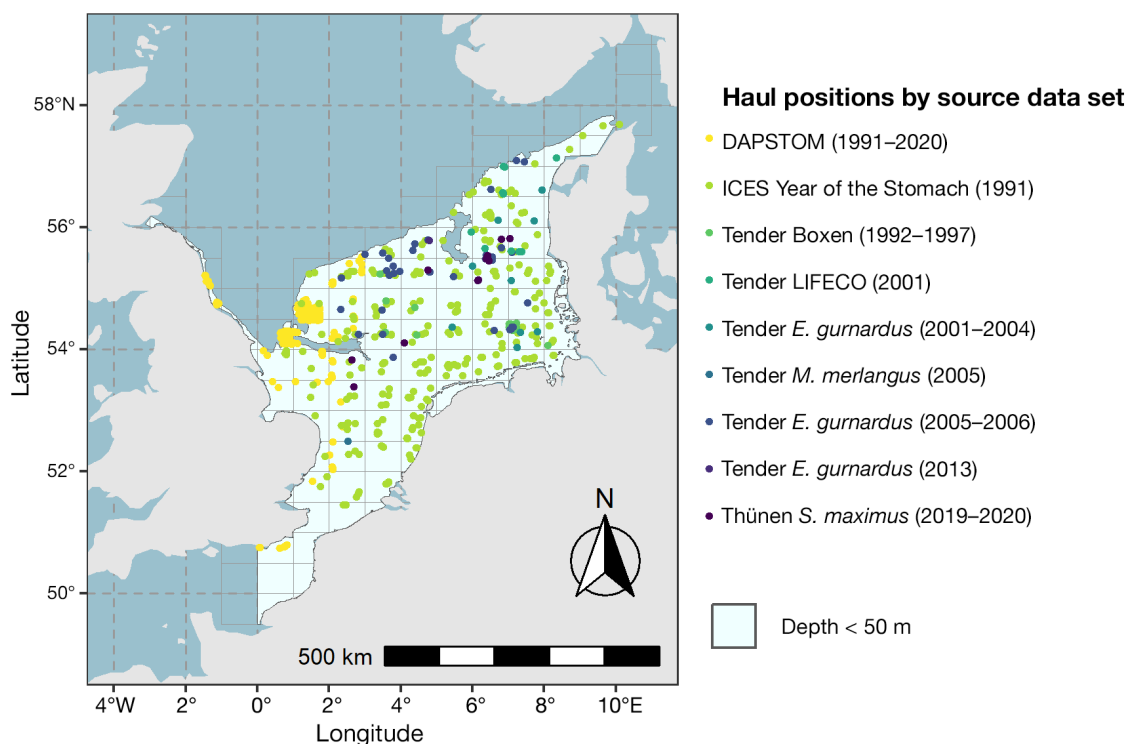

Fig. 1. North Sea, showing the haul positions of the stomach content data used in the present study after data cleaning and standardization, colour-coded by the data sets from which they originated. The study area is bounded to the northwest by the 50 m depth contour. 'Thünen *S. maximus*' refers to unpublished data by M. Bernreuther

tures through stronger thermal stratification, while the southern North Sea experiences higher mixing and, thus, temperature variability (Núñez-Riboni & Akimova 2015, Schrum et al. 2016).

2.2. Data

2.2.1. Fish stomach content data

Fish stomach content data were compiled from different sources (Fig. 1; Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m739p173_supp1. pdf), spanning the time period between 1991 and 2020. They included data from the 'Year of the Stomach 1991' of the International Council for the Exploration of the Sea (ICES) (ICES 1991, 1997) and the Integrated Database and Portal for Fish Stomach Records (DAPSTOM) of the Centre for Environment, Fisheries and Aquaculture (Cefas) (Pinnegar 2014), as well as data collected during annual survey campaigns in the North Sea for EU tenders (Huwer et al. 2014) and available data from previous studies (Hinz et al. 2005, Schückel et al. 2011, 2012, 2013, M. Bernreuther unpubl. data; Fig. S1). The records were standardized and harmonized to a consistent data set (see also Text S1: 1.1.1. Fish stomach content data). Predators were subdivided by life stage to account for possible ontogenetic variability in diets ('juvenile' and 'adult' classes, with the species-specific length at maturity serving as a threshold; Table S2). Species for which no length at maturity is known were removed (lesser weever *Echiichthys vipera* and rock gunnel *Pholis gunnellus*). For each individual fish, relative prey composition was calculated based on prey weight (%W) as a proxy for energetic contribution (Hyslop 1980, Buckland et al. 2017). Since this study focused on demersal fishes, pelagic fishes (herring, sprat, mackerel, horse mackerel) were excluded from the analysis in their role as predators, as were generally all species for which zooplankton constituted a large part of the diet (>35% of total prey weight). Furthermore, predator stomach contents in which a large proportion (>35% of total prey weight) of prey was unidentified or reported at a highly integrated taxonomic level were excluded. At the end of this filtering process (see also Fig. S2), any predator/life stage combination (Pred/ LS) that was represented by fewer than 15 individuals was removed to ensure a minimum level of replication. Through the data collation and filtering process, suitable stomach data were obtained for 13 Pred/LS combinations across 8 species: grey gurnard (juvenile + adult), cod (juvenile + adult), greater sandeel (adult), common dab (adult), haddock (juvenile + adult), whit-

ing (juvenile + adult), plaice (juvenile + adult), and turbot (adult). The number of stomachs available per Pred/LS varied between 17 for turbot and 1242 for adult whiting.

To identify alternative feeding strategies, Schoener's index (D) for diet overlap was calculated:

$$D = 1 - 0.5\left(\sum_{i=1}^{n} \left| p_{x_i} - p_{y_i} \right|\right) \qquad (1)$$

where p_x and p_y are the proportions of a given prey type i in Pred/LS x and y (Schoener 1968). The calculation was performed based on the mean relative weight (%W) of each prey type per predator, only considering prey types that had been recorded in at least 8 stomachs per Pred/LS combination. Following the recommendation made by Wallace & Ramsey (1983), a given overlap was deemed biologically significant if $D > 0.6$ (compare to Schückel et al. 2012). Schoener's index for diet overlap was calculated using the R package 'FSAmisc' (Ogle 2022).

For RLQ and fourth-corner analyses, juvenile life stages of predators were excluded due to a lack of trait information, as was turbot due to low sample size (n = 17). The sample size of the second least represented predator species (haddock, n = 52) acted as a point of reference, and a random subset of 52 stomachs was drawn from each of the other predator species to achieve an equal representation of each species for the permutation tests conducted in fourth-corner analysis. This reduced data subset will hereafter be referred to as 'analysis data set' in contrast to the 'complete data set' containing all predator stomachs and life stages held over after the filtering process. The analysis data set was transformed into a diet matrix, giving the relative prey composition (% weight, compare to Spitz et al. 2014) per individual fish.

2.2.2. Trait data

Trait data were compiled for predator fishes and their prey (Table 1; Table S1). Predator traits reflected aspects of prey encounter and handling (maximum length, relative maxillary jaw length), energetic requirements (energy density, protein content, omega-3 content, aspect ratio), and life history (von Bertalanffy growth coefficient). Predator (maximum) length is reported to correlate with the favoured prey size (e.g. Floeter & Temming 2003, Trenkel et al. 2005, Reecht et al. 2013), while relative maxillary jaw length, i.e. the ratio between maxillary upper jaw length and head depth measured at eye height, is a proxy for gape size,

Table 1. Predator and prey traits included in the study. Selection was based on literature and considerations on which traits might influence a predator—prey interaction. Predator traits are all continuous, prey traits are partly continuous (maximum length, energy density) and partly categorical (body shape, texture, protection, mobility, habitat). WM: wet mass

Trait	Functional implication	Unit/class	Range and example taxa
Predator			
Maximum length	Predator—prey size ratio	cm	40 (greater sandeel) to 140 (cod)
Aspect ratio	Consumption rate	Unitless (ratio)	0.97 (whiting) to 1.77 (turbot)
Relative maxillary jaw length	Gape size	Unitless (ratio)	0.28 (plaice) to 1.75 (greater sandeel)
von Bertalanffy growth coefficient	Life history strategy	yr^{-1}	0.15 (plaice) to 0.4 (greater sandeel)
Energy density	Dependence on prey?	$kJ\ g_{WM}^{-1}$	3.36 (turbot) to 6.1 (grey gurnard)
Protein content	Demand for growth	$g\ 100\ g_{WM}^{-1}$	16 (dab) to 18.6 (turbot)
Omega 3 content	Reaction to visual cues, swimming capabilities	$g\ 100\ g_{WM}^{-1}$	0.351 (dab) to 1.79 (whiting)
Prey			
Maximum length	Handling by predator	cm	0.6 (two-toothed Montagu shell *Kurtiella bidentata*) to 140 (cod)
Energy density	Bioenergetic value	$kJ\ g_{WM}^{-1}$	0.13 (tubularian hydroids) to 11.45 (herring *Clupea harengus*)
Body shape	Handling by predator	Flat Round Elongated Compressiform	Plaice, ophiuroids Lump fish *Cyclopterus lumpus* Sandeel, polychaetes Mussels of the genus *Abra*
Texture	Digestibility and ingestion potential for predator	Soft Medium Hard Very hard	Polychaetes Sandeel Echinoderms, crabs Mussels of the genus *Abra*
Protection	Strategies to increase predation cost for predator	Chemical defence Physical defence Counterattack Escape Hiding	Lesser weever *Echiichthys vipera* Echinoderms Crabs Clupeids, loliginid squid Hermit crabs, flatfish
Mobility	Escape potential in an interaction	Immobile Low Medium High Very high	Sponges, ascidians Caprellid amphipods Scaldfish *Arnoglossus laterna* Whiting Clupeids, loliginid squid
Habitat	Encounter probability between predator and prey	In seafloor On seafloor Benthopelagic Pelagic	Polychaetes of the family Nereididae Hooknose *Agonus cataphractus* Herring Sardine *Sardina pilchardus*

determining the maximum ingestible prey size (Piet et al. 1998, Su et al. 2019). Energy density is hypothesized to depend on prey energy density, while contents of protein and fatty acids are linked to physiological properties of predatory fishes. High omega-3 polyunsaturated fatty acid (PUFA) content positively influences swimming capabilities and neuronal development, reducing the reaction time to visual cues (Bell et al. 1995, Fuiman & Perez 2015, Gladyshev et al. 2018). After water, proteins typically constitute the second-largest part (10—25%) of the body weight of a fish, and the uptake of protein-rich prey enhances fish growth (Ahmed et al. 2022). The aspect ratio, i.e. height of the caudal fin divided by its surface area, is a predictor of consumption rates in fishes, with high aspect ratios typically found for fast swimmers with high energy expenditure (Pauly 1989). The von Bertalanffy growth coefficient relates to predator population dynamics and, hence, predation pressure on a given prey (compare to Gravel et al. 2016). Other predator traits deemed potentially informative for predator—prey interactions (e.g. maxillary jaw to body length ratio, age at maturity) were not considered due to collinearity with the remaining traits. Collinearity was evaluated by calculating pairwise Spearman's correlations and comparing the outcomes in multipanel scatterplots (Zuur et al. 2010). The

exclusion threshold was a correlation coefficient of 0.7, leading to the removal of highly correlated traits. One exception was made for the traits 'relative maxillary jaw length' and 'von Bertalanffy growth coefficient' (r = 0.72), which were correlated due to one species (greater sandeel) scoring particularly high in both traits, while the values for all other species did not indicate a relationship between them.

Two continuous (maximum length, energy density) and 5 categorical traits (body shape, texture, protection, mobility, habitat) were selected for prey (Table 1, including example taxa; Table S3). Maximum length (or diameter, for radial symmetry) affects handling by a predator (Floeter & Temming 2003, Pinnegar et al. 2003, Reecht et al. 2013). Energy density provides an overall indication of a prey's bioenergetic value (e.g. Andersen 2001). Regarding body shape, which affects prey handling, species were classified as 'round', 'elongated', 'flat', or 'compressiform'. Texture determines digestibility, and was categorized based on hard body structures: 'soft' (no structures), 'medium' (endoskeleton but no external protective layer), 'hard' (chitinous exoskeleton or external bony plates), and 'very hard' (calcareous structures including shells). Protection refers to strategies for predation evasion, classified as 'chemical defence', 'physical defence', 'counter attack', 'escape', and 'hiding'. Mobility refers to escape abilities, spanning from 'immobile', 'low', 'medium', and 'high' to 'very high'. Finally, the trait 'habitat', determining encounter probability, was categorized as 'pelagic', 'benthopelagic', or as living 'on seafloor' or 'in seafloor'.

Predator and prey trait data were compiled at the species level from pre-existing trait databases, specifically Beukhof et al. (2019a), FishBase (Froese & Pauly 2022), SeaLifeBase (Palomares & Pauly 2022), WoRMS (WoRMS Editorial Board 2022), and MarLIN (MarLIN 2022), as well as primary and secondary literature. Categorization of prey species in the cases of the traits 'protection' and 'mobility' was performed based on expert judgement in due consideration of the literature. Protection strategies were deduced from information regarding morphology (e.g. camouflage, spikes) and behaviour, while mobility was derived from information on swimming speed, which was found for a few species and used to infer mobility categories for closely related or ecologically similar species. The morphometric predator trait 'relative maxillary jaw length' was measured based on scientific drawings, using the software ImageJ (version 1.53o, Rasband 1997–2018) (compare Toussaint et al. 2016, Su et al. 2019). Regarding continuous traits, some information gaps occurred due to lacking taxon-specific data. Amongst predator species, this concerned aspect ratio for greater sandeel and energy density for grey gurnard. In the case of continuous prey traits, information gaps primarily occurred in energy density (81% of taxa), while maximum length was missing for only a few taxa (15%). Data gaps were filled with information from (closely) related taxa as best available estimates or based on expert judgement (see Supplement 2 at www.int-res.com/articles/suppl/m739p173_supp2.xlsx).

Prey maximum length and energy density were highly skewed towards the low end of the spectrum. Since RLQ ordination involves single-table ordination of matrices **R** and **Q** using a Hill-Smith ordination, which for continuous variables is equivalent to a principal component analysis (Hill & Smith 1976), a more normal-like distribution of continuous traits was desired to avoid strong effects of extreme values (Legendre & Legendre 2012), and the 2 traits were therefore $\log_{10}$-transformed.

2.2.3. Survey data on prey availability in the field

Fish and benthos survey data were compiled for the study area and period (1991–2020) to assess prey availability in the field. Data compiled during the ICES North Sea International Bottom Trawl Survey (NS-IBTS) (ICES 2020) were collated from the Thünen Institute's database and the Database of Trawl Surveys (DATRAS; ICES 2022). These data were supplemented with data from the German Small-scale Bottom Trawl Survey (GSBTS; for a survey description, see Ehrich et al. 2007). Both surveys are conducted annually in summer (between July and September), using the same vessel ('Walther Herwig III', only refers to the part of NS-IBTS sampled by Germany), gear (Grand Ouverture Vertical otter bottom trawl), and protocol. The GSBTS generally samples 12 so-called 'boxes', fixed quadrats of 10 × 10 nautical miles that are distributed across the North Sea, and in which typically 21 hauls are performed to collect high-resolution data on demersal fish biodiversity, abundance, and biomass. From the GSBTS, only fish abundance data collected in Box A were included in this study (see also Text S1: 1.1.2. Survey data on prey availability in the field).

Data on benthic epi- and infauna were provided by Senckenberg am Meer, which performs an annual sampling scheme during the German sampling campaign for NS-IBTS and GSBTS onboard the RV 'Walther Herwig III'. Epifauna data were collected using a 2 m beam trawl, sampling for ~5 min at a target speed of 2 knots over ground, while infauna was sampled

with a 0.1 m^2 Van Veen grab sampler. In parallel to the NS-IBTS hauls, 1 station was sampled per ICES statistical rectangle with each method. In Box A of the GSBTS, a target number of 9 hauls was performed by beam trawl and up to 9 stations were sampled by grab.

Furthermore, prey field abundance data for fish and benthos were available from a combined fish and benthos sampling campaign to the Dogger Bank, conducted in May 2006 (Cruise WH287 of RV 'Walther Herwig III'). Here, data were collected at 35 stations, using the same methods as on the NS-IBTS and GSBTS surveys (Weinert et al. 2010, Sell & Kröncke 2013). Abundance data for fish and benthic species were standardized to count per 1000 m^2 to obtain comparable units between the organisms.

2.3. Analysis

A challenge in the assessment of correlations between predator and prey traits is that they cannot be measured directly; they only become apparent indirectly through the proportions of prey types with different traits across predators with varying characteristics. This problem has been described analogously for the linkage of species traits to environmental conditions and was termed 'the fourth-corner problem' (Legendre et al. 1997). With the fourth-corner approach, a solution to this problem was proposed, linking matrices **R** (predator traits) and **Q** (prey traits) by applying a 2-step permutation model ('model 6', Dray & Legendre 2008) to the diet matrix, i.e. matrix **L**. In this model, associations of predator and prey traits with the diet matrix are initially tested separately (permuting rows and columns, respectively, of **L**), and pairwise Pearson correlation coefficients between predator and prey traits are subsequently returned in a fourth matrix (**D**), figuratively filling the 'fourth corner' (Legendre et al. 1997, Dray & Legendre 2008).

RLQ ordination is a double-co-inertia ordination method. First, a correspondence analysis (CA) of matrix **L** is performed. The obtained row and column weights are then used as weights in single-table ordinations of **R** and **Q**, maximizing their respective inertia. Finally, the actual RLQ ordination utilises the 3 single-table ordination outcomes to combine them in a single, dimensionally-reduced ordination space by maximizing the covariance between matrices **R** and **Q** (Dolédec et al. 1996). The complementary nature of fourth-corner and RLQ analyses prompts the combination of the 2 approaches, one for significance tests and one for visualization (Dray et al. 2014). The projected inertia describes the amount of covariance between matrices **R** (predator traits) and **Q** (prey traits) captured by the RLQ axes compared to independent ordinations of the 2 matrices, and therefore provides information about the representativeness of the analysis outcomes (compare Dolédec et al. 1996, Dray et al. 2003).

Prior to the analysis, continuous trait data (all predator traits and the 2 log$_{10}$-transformed prey traits 'length' and 'energy density') were z-transformed. For fourth-corner analysis, 9999 permutations were run, and p-values ($\alpha = 0.05$) were corrected for multiple testing using the false discovery rate (FDR) method (Benjamini & Hochberg 1995). The single-table ordination method applied to matrices **R** and **Q** depends on the data formats of the trait data. Matrix **R** consisted entirely of continuous variables, while matrix **Q** constituted a mix of continuous and categorical variables. For matrix **R**, single-table ordination was therefore performed using PCA, and matrix **Q** was ordinated using Hill-Smith analysis (Hill & Smith 1976, compare to Dray et al. 2014).

To cluster predator and prey traits, a k-means clustering routine was performed on the scores of the first 2 RLQ axes (compare Spitz et al. 2014). The number of clusters was determined *a priori* based on the within-cluster sum of squares.

To assess prey preferences, the validity of the fourth-corner and RLQ results in light of actual selectivity was assessed by calculating Chesson's α, an electivity index ranging between 0 and 1:

$$\alpha_i = \frac{r_i/p_i}{\sum_i r_i/p_i} \tag{2}$$

where relative preference α for prey item i is a function of the relative abundance of i in the stomach (r_i) and in the environment (p_i). An α equal to one divided by the number of available prey types indicates random feeding (Chesson 1978, Lechowicz 1982).

The complete data set of stomach content data was combined with the fish- and benthic field survey data, and matching stations (matching by Country, Vessel, Year, Trip, Station, and Date) were extracted. From both data sets, prey abundance data were used instead of weight data, as Chesson's α is an abundance-based method. Prior to analysis, the stations were categorized by the availability of prey field data in terms of prey components (fish, epifauna, infauna, and combinations thereof). This processing step showed that, for most stations, only fish field data were available. Merely 12 stations with records of both epifauna- and fish field data could be identified, for which, in turn, stomach data were only available for grey gurnard. To allow for comparisons between predators, electivity index cal-

culations were therefore limited to fish prey, for which 150 hauls and 8 Pred/LS combinations were available, hereafter referred to as the 'electivity data set'. Chesson's α was calculated station-wise and then averaged for each Pred/LS and associated prey type, adopting a threshold sample size of 8 per predator × prey combination as a basis for average calculations (leading to the exclusion of grey gurnard and haddock juveniles due to low sample sizes). To distinguish preference from unselective feeding, Chesson's α for random feeding (Chesson's α_{random}) was averaged across all stations where a given Pred/LS combination had been sampled. Because this analysis had to be limited to fish diets, relative prey abundance was calculated, with 100% representing total fish prey instead of total prey, both in the stomach and field. The 95% confidence interval (CI) was determined and used to interpret electivity indices, considering electivity significant if the 95% CI did not include the value of Chesson's α representing random prey choice (Bernal et al. 2015).

Electivity calculation was based on prey abundance, while RLQ and fourth-corner analyses were based on prey weight proportions. To relate the outcomes of both analyses, Pearson correlation tests were used to test the mutual resemblance of the patterns in relative prey weight and relative prey number in the electivity data set.

All analyses were performed in R v.4.2.2 (R Core Team 2019). For RLQ ordination and fourth-corner analysis and clustering, the packages 'ade4' (Dray & Dufour 2007), 'factoextra' (Kassambara & Mundt 2020), and 'cluster' (Maechler et al. 2019) were used. Chesson's α was calculated using the R package 'electivity' (Quintans 2019). Visualizations were prepared using 'ggplot2' (Wickham 2016).

3. RESULTS

3.1. Diet composition and diet overlap

Relative diet compositions (%W) revealed a variety of prey spectra for the 13 Pred/LS combinations (Fig. 2). Divergences in average weight-based diet composition were most evident when considering the relative proportions of fish and benthic prey. Six Pred/LS consumed primarily fish prey (turbot adults = 94.8%; whiting adults = 69.7%; greater sandeel adults = 64.3%; plaice adults = 63.4%, whiting juveniles = 59%, grey gurnard adults = 57.1%), while 5 Pred/LS ate mostly benthic invertebrates (common dab adults = 84.6%; haddock adults = 82.5%; cod juveniles = 79.8%; grey gurnard juveniles = 73.3%; haddock juveniles = 72.8%). Two Pred/LS had a rather balanced diet composition (% fish and % benthos in diets: cod adults = 45.2 and 52.9%; plaice juveniles = 48.8 and 46.3%).

Assessment of diet overlaps with Schoener's D revealed that, although some similarities in the diet existed across life stages of individual predator species and between different species, significant overlaps were rather rare (Table 2). Three species showed signifi-
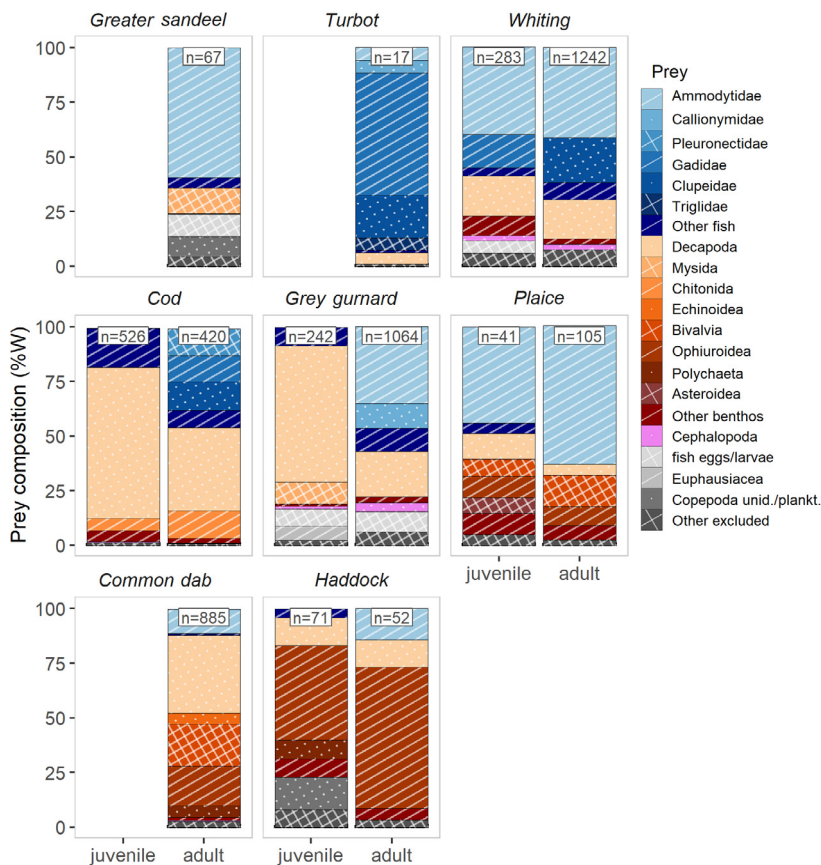

Fig. 2. Prey composition (by relative weight, %W) of 8 fish predator species in the southern North Sea, distinguished by life stage (juvenile, adult). Prey types were integrated to higher taxonomic groups. n indicates the stomach sample size available per predator/life stage combination. Fish and benthic invertebrate prey are depicted in shades of blue and orange, respectively, and cephalopods in violet. Items that were not considered in subsequent analysis steps are shown in grey shades. Prey types that individually constituted <5% of relative prey composition are pooled as 'Other fish', 'Other benthos', and 'Other excluded'

cant diet overlap between juvenile and adult stages (Table 2): plaice ($D = 0.79$), whiting (0.74), and haddock (0.68). The diets of whiting juveniles and adults furthermore overlapped with those of adult grey gurnards (0.76 and 0.68) and juvenile plaice (0.64 and 0.65). Adult plaice and adult greater sandeel were somewhat congruent (0.66), as were juvenile grey gurnards and cod (0.71). Common dab and turbot diets did not overlap significantly with those of other species (for further detailed information, see Text S2).

3.2. Predator–prey trait associations

RLQ ordination returned 2 principal RLQ axes (RLQ1 and RLQ2), accounting for 57.9 and 21.9% of projected inertia, respectively (Fig. 3; Table S4). RLQ1 was negatively correlated with the predator traits omega-3 content ($r = -0.52$, $p_{adjusted} = 0.001$) and relative maxillary jaw length ($r = -0.37$, $p_{adjusted} = 0.007$; Fig. 3b), as well as with prey energy density ($r = -0.44$, $p_{adjusted} = 0.002$; Fig. 3c), but was positively correlated with prey of 'low' mobility ($r = 0.51$, $p_{adjusted} = 0.002$). Only the predator trait maximum length was (negatively) associated with RLQ2 ($r = -0.36$, $p_{adjusted} = 0.020$; Fig. 3b).

K-means clustering grouped predator and prey traits into 3 clusters (Fig. 3; Table S5), each characterized by at least 1 of the traits that correlated with the RLQ axes. Cluster 1 included prey of 'low' mobility, Cluster 2 was defined by predators with high omega-3 content and large relative maxillary jaw length, and by prey with high energy density. Cluster 3 corresponded to predators with large maximum length.

Amongst the traits, significant associations were limited to a positive relationship between predator omega-3 content and prey energy density ($r = 0.5$, $p_{adjusted} = 0.008$, both positioned within Cluster 2, see also Fig. S3), and a negative correlation between high predator omega-3 content and the category 'low' of the prey trait mobility ($r = -0.48$, $p_{adjusted} = 0.008$, Cluster 1). Given the ordinal nature of this prey trait and the positioning of its modalities along RLQ1 ('immobile' and 'low' on the positive end, 'medium', 'high', and 'very high' on the negative end), a generally positive association of prey mobility and predator omega-3 content is assumed. The predator traits relative maxillary jaw length and maximum length, although significantly associated with RLQ1 and RLQ2, respectively, were not correlated with any prey traits.

When considering predator and prey ordination in terms of taxonomy rather than traits along the same RLQ axes (Fig. 4), the first axis sorted predators from piscivorous (negative end) via generalist (close to 0) to benthivorous predators (positive end). The pattern was echoed by the prey organisms, lining up fishes (negative end) via cephalopods and decapods (generalist) to benthic organisms (polychaetes, echinoderms, and bivalves, positive end) along the first RLQ axis. The second axis ordinated predator species by maximum length, but without a clear pattern regarding prey taxa.

3.3. Prey electivity

Adult grey gurnards consumed Ammodytidae (sandeels) at a higher percentage than present in the ambient prey assemblage ($\alpha = 0.45 \pm 0.32$ 95%CI, Fig. 5). The same was the case for adult whiting ($\alpha = 0.63 \pm 0.43$ 95%CI), which also actively selected clu-

Table 2. Schoener's diet overlap (D), ranging from 0 (no overlap) to 1 (perfect overlap). $D \geq 0.6$ is deemed biologically significant (highlighted in **bold**). a: adult; j: juvenile

|		Cod		Dab	Greater sandeel	Grey gurnard		Haddock		Plaice		Turbot	Whiting	
		a	j	a	a	a	j	a	j	a	j	a	a	j
Cod	a	1.00												
	j	0.51	1.00											
Dab	a	0.38	0.38	1.00										
Greater sandeel	a	0.0	0.0	0.12	1.00									
Grey gurnard	a	0.26	0.26	0.38	0.55	1.00								
	j	0.43	**0.71**	0.38	0.2	0.36	1.00							
Haddock	a	0.14	0.14	0.44	0.16	0.29	0.14	1.00						
	j	0.16	0.16	0.41	0.1	0.16	0.16	**0.68**	1.00					
Plaice	a	0.06	0.06	0.42	**0.66**	0.49	0.06	0.3	0.15	1.00				
	j	0.15	0.15	0.48	0.55	0.58	0.15	0.42	0.27	**0.79**	1.00			
Turbot	a	0.34	0.05	0.11	0.06	0.17	0.05	0.11	0.05	0.11	0.11	1.00		
Whiting	a	0.37	0.22	0.34	0.5	**0.68**	0.23	0.29	0.16	0.56	**0.65**	0.31	1.00	
	j	0.36	0.23	0.35	0.56	**0.76**	0.31	0.29	0.16	0.55	**0.64**	0.3	**0.74**	1.00
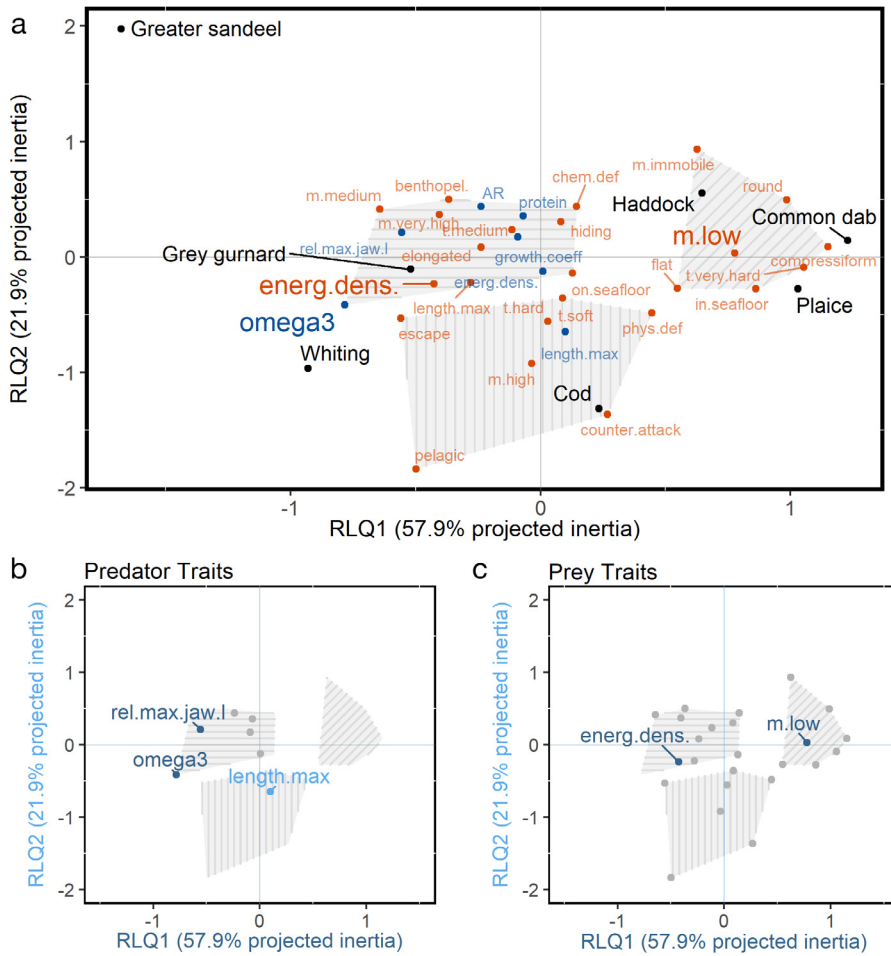
Fig. 3. Results of RLQ ordination and fourth-corner analysis. (a) Positions of predator (blue) and prey (orange) traits along the first and second RLQ axes, together with coordinates of predator species (black dots). Traits between which significant correlations were found are emphasised (magnified, **bold**): predator omega-3 content (omega3), prey energy density (energy.dens.), 'low' mobility in prey (m.low). Trait clusters are depicted as cross-hatched grey polygons. (b) Predator traits and (c) prey traits that were significantly correlated with the first (dark blue) and second RLQ axis (light blue). Non-correlating traits are indicated by grey points

peids as prey (α = 0.80 ± 0.30 95%CI). With regards to cod, juveniles showed a preference for gobies (Gobiidae) (α = 0.56 ± 0.41 95%CI), while adults preferred gadoids (α = 0.42 ± 0.30 95%CI), especially whiting (α = 0.18 ± 0.06 95%CI), and dab (α = 0.13 ± 0.05 95%CI). Adult turbot and juvenile whiting did not show significant prey preferences.

3.4. Synthesis of RLQ ordination, fourth-corner analysis, and electivity results

The trait profiles of 4 important predatory North Sea fish species (adults only) and the trait profiles of their associated prey were compared with the results from electivity analysis, using the electivity data set in which both prey abundance and weight were included

(Fig. 6). Relative prey abundances (used to calculate preferences) and relative prey weights (used for trait-based analysis) were closely correlated in all 4 predators within the data set, as confirmed by the Pearson correlation tests (grey gurnard: r = 0.96, p < 0.001; cod: r = 0.97, p < 0.001; whiting: r = 0.94, p < 0.001; turbot: r = 0.99, p < 0.001). Therefore, in combination with the information drawn from prey electivity calculations, the ranking of prey types given in Fig. 6 is assumed to represent prey importance. In terms of the predator trait omega-3 content, a gradient can be drawn from turbot via cod and grey gurnard to whiting. The main prey items of cod (the swimming crab *Macropipus tuberculatus,* dab, whiting, and the masked crab *Corystes cassivelaunus*) showed a mixed trait profile, with energy density being in the medium range, and prey mobility ranging widely between 'high' and 'low'. For
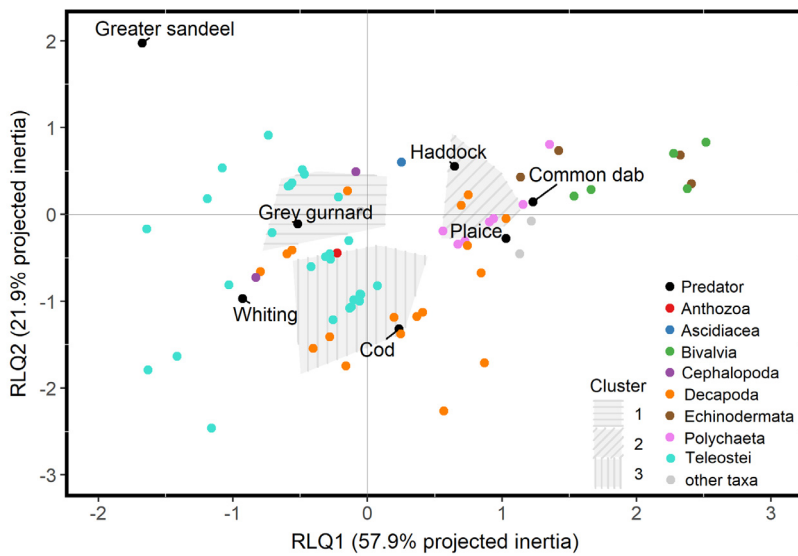
Fig. 4. Positions of predator (black dots) and prey taxonomic groups (dots colour-coded by group) along the RLQ axes. The 3 clusters (hatched grey polygons) resulting from *k*-means clustering performed on the predator and prey traits are given for orientation (compare Fig. 3)

whiting and grey gurnard, energy-dense prey consisted primarily of clupeid fishes, for which adult whiting furthermore showed a clear preference (Chesson's α). Whiting and grey gurnard fed primarily on prey types with 'high' or 'very high' mobility. Turbot had a fish-based diet with prey types of high energy density and 'high' to 'very high' mobility, despite its low omega-3 content.

4. DISCUSSION

In this study, diet data and species characteristics data were used to investigate general trait associations between demersal fishes and their (benthic/fish) prey and to identify key traits associated with predator—prey
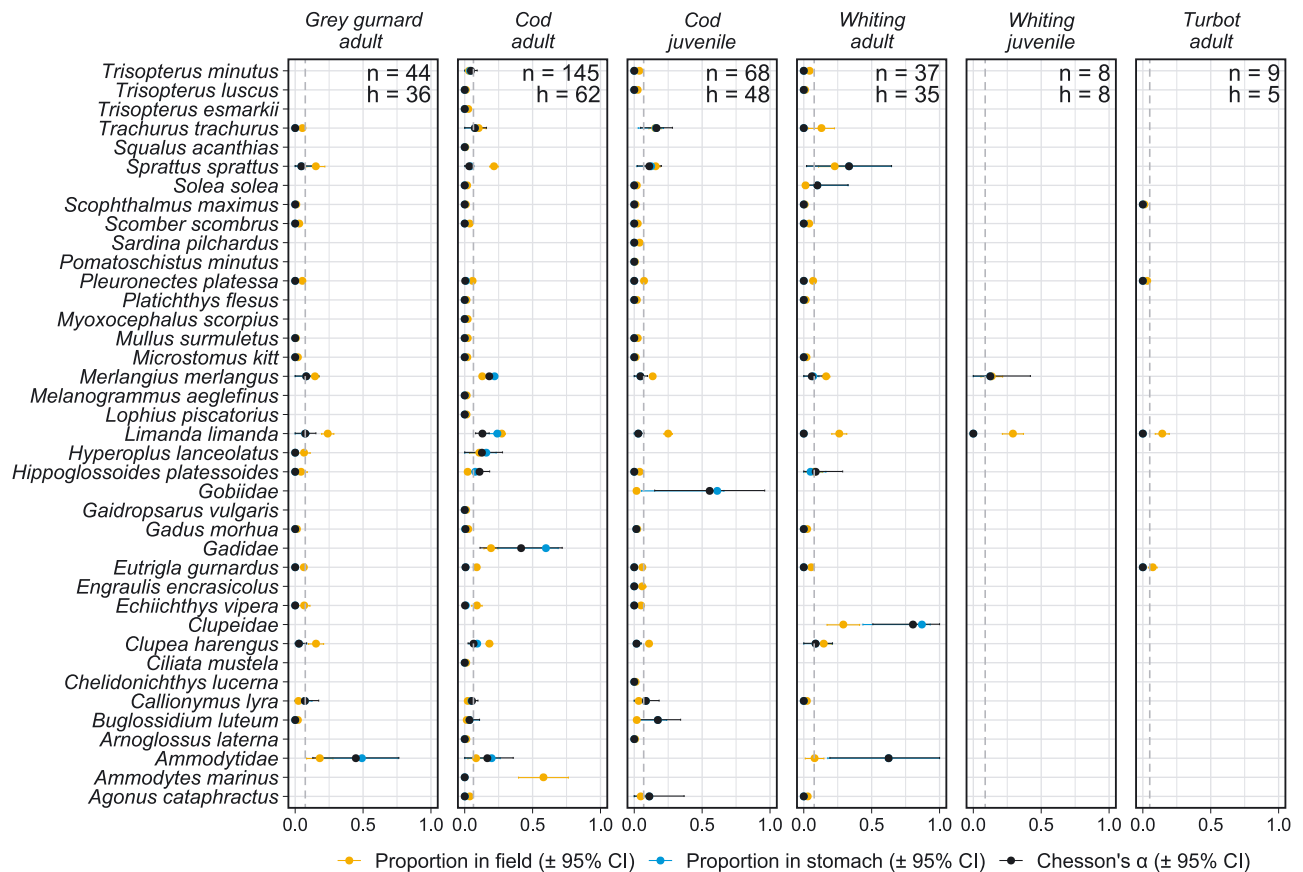

Fig. 5. Mean Chesson's α (±95% confidence interval) for each prey type, calculated per predator/life stage combination (Pred/LS). Mean Chesson's α for random feeding (Chesson's $α_{random}$) is represented by a vertical dashed grey line. For each prey type, the mean (±95% CI) proportions in the field (yellow) and in the stomach (blue) are indicated. n refers to the total number of individuals included in electivity-index calculation per Pred/LS, while h indicates the number of different hauls from which these individuals were taken
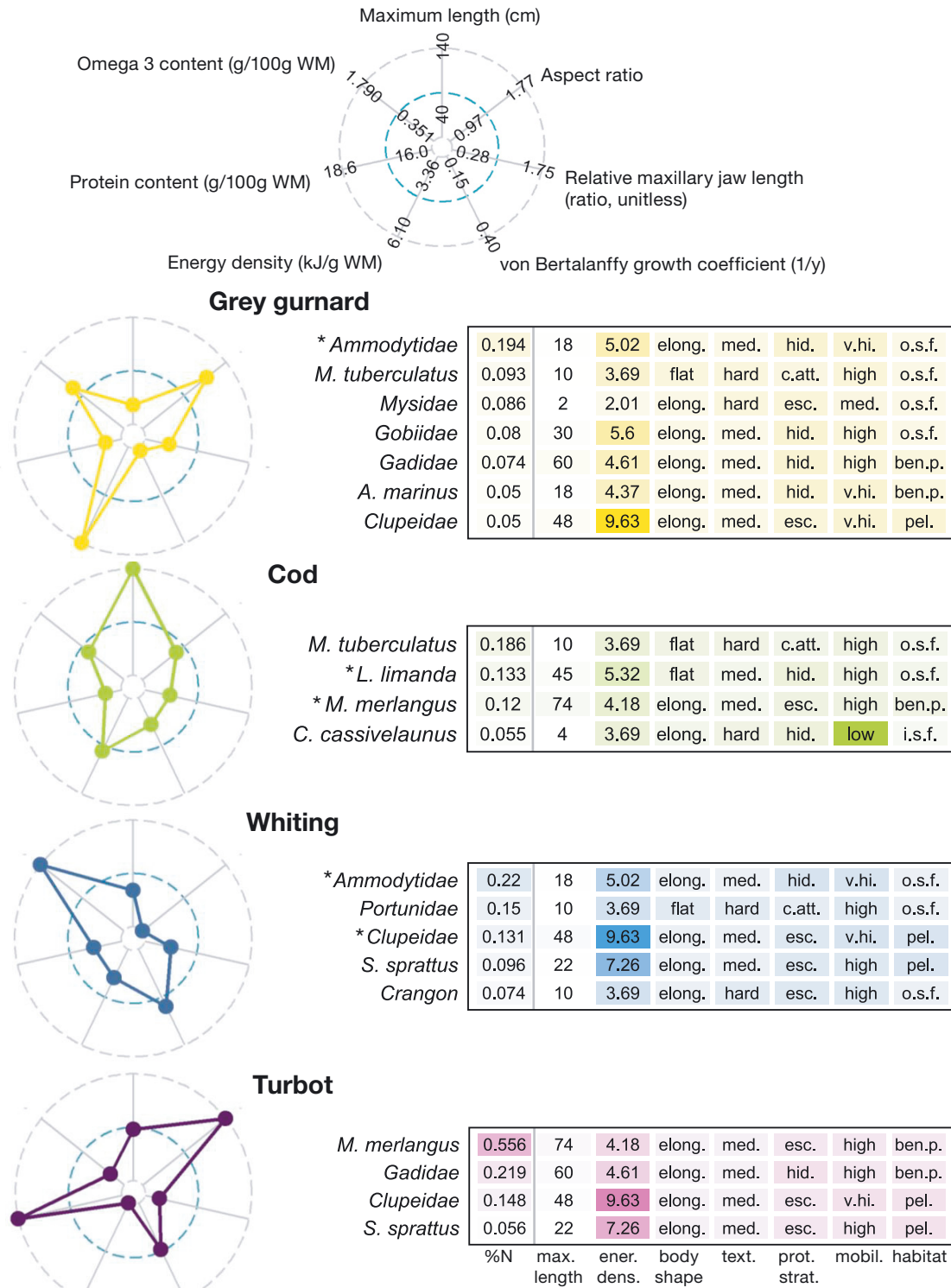
Fig. 6. Comparison of the trait profiles of 4 demersal fish predators (grey gurnard, cod, whiting, turbot) with the trait profiles of their prey (prey categories that each contributed ≥5% to overall abundance). Radar charts visualize the (adult) predator trait profiles (the traits and their ranges are indicated at the top) while prey traits are indicated in tables. Prey trait profiles are sorted by relative abundance (%N) in the stomachs of the respective predator species, descending from most to least abundant prey. Colouration highlights those prey traits that correlated with omega-3 content in fourth-corner analysis: energy density (gradient) and 'low' mobility (discrete). Prey types with a Chesson's α indicating significant prey preference are marked with an asterisk. Prey trait abbreviations: ener. dens. = energy density, text. = texture, prot. strat. = protection strategy, mobil. = mobility. Prey trait categories are abbreviated (in order of appearance) as elong. = elongated, med. = medium, hid. = hiding, c.att. = counter attack, esc. = escape, v.hi. = very high, o.s.f. = on seafloor, ben.p. = benthopelagic, pel. = pelagic, i.s.f. = in seafloor

interactions. In doing so, and by comparing our results to taxon-based electivity indices and diet compositions, we aimed to test the suitability of RLQ and fourth-corner analysis for describing feeding interactions between North Sea fishes and their prey on a purely functional level. The findings are discussed in light of previous diet studies on demersal North Sea fishes and are related to the ecological basis of the identified trait associations.

4.1. Diet composition and prey preferences

Overall, the findings for predator diet compositions in this study corresponded well with previous reports, thus delivering a representative foundation for trait-based analysis (a detailed comparison of observed and previously reported diets is provided in Table S6). Especially sandeels were confirmed as a primary food source (compare to Daan et al. 1990, Engelhard et al. 2008, 2013) and found in large proportions (>30 %W) in 6 out of 13 Pred/LS combinations analysed.

The limited overlap between diets of different predators, as demonstrated by Schoener's index, supported the existence of alternative feeding strategies. A trait-based analysis of feeding strategies would have been little informative in cases of high diet overlap, which would have suggested that prey composition is invariant between predators with varying trait profiles. Instead, predator–prey associations were corroborated by the significant prey preferences of grey gurnards, cod, and whiting, as identified using Chesson's α. These are even more noteworthy given that the lack of co-sampled fish stomachs and benthic-invertebrate field data limited electivity analyses to fish prey.

While the compiled diet data corresponded well with previous observations of diet compositions, it must be noted that this study is based on the integration of diet data sampled across various depths and habitats, with the goal to capture fundamental trait connections. Intraspecific variability over space and time was therefore not accounted for in our analysis. Our integrated approach is neither meant to nor suitable to resolve spatial differences which relate to the fact that water depth and habitat type change prey availability, particularly for demersal fish (Sell & Kröncke 2013, Giraldo et al. 2017, Timmerman et al. 2021). Intraspecific variability, which we know occurs in the field (e.g. Hinz et al. 2005, Weinert et al. 2010, Cachera et al. 2017) is also not evaluated through our approach, which identifies the typical, overall relationships, rather than their variability.

4.2. Predator–prey trait associations

Fourth-corner analysis indicated a trait link between predator omega-3 content and the prey trait energy density, as well as with prey mobility, offering a functional explanation to observed predator–prey ordination patterns. To assess the ecological relevance of the identified associations, it is necessary to revisit the meaning of these traits in the context of a predator–prey relationship. Prey energy density is a measure of value for a given predator, as energy-rich prey facilitates growth and reproduction. Omega-3 PUFAs, and here especially docosahexaenoic acid (DHA), are known to promote reduced reaction times to visual cues, as well as increase the capacity for sustained and burst swimming (Bell et al. 1995, Fuiman & Perez 2015, Gladyshev et al. 2018).

Optimal foraging theory states that predator feeding preferences are the result of a trade-off between the (energetic) prey value for the predator's fitness and the cost of consumption (search time, pursuit, handling) (Townsend & Winfield 1985). Among all prey types included in the RLQ and fourth-corner analyses, clupeids are particularly energy-rich (Pedersen & Hislop 2001). The family Clupeidae consists of free-swimming pelagic or benthopelagic swarming fishes (in the southern North Sea mainly herring and sprat) which can reach high swimming speed during escape (e.g. Blaxter 1990), requiring high energy expenditure by a predator to capture them. Thus, predators with better swimming capacities and faster responses to visual prey cues are better 'equipped' to prey on this energy-rich and highly mobile prey. At the same time, clupeids contain high amounts of omega-3 PUFAs in their flesh themselves (Calder & Yaqoob 2009, Rubio-Rodríguez et al. 2010), and since omega-3 PUFAs are a group of fatty acids that fishes cannot produce themselves and therefore source from their diet (Rubio-Rodríguez et al. 2010), variation in omega-3 content between predators might both reflect the ability and the consequence of consuming energy-rich prey.

No association was found between prey and predator maximum length, although expected, given the widely acknowledged (positive) predator–prey size relationship (Ursin 1973, Scharf et al. 2000, Floeter & Temming 2003, 2005, Pinnegar et al. 2003). Similarly, another presumably significant relationship was not found, namely the association of prey maximum length and predator relative maxillary jaw length, which serves as a proxy for gape size (compare Toussaint et al. 2016, Su et al. 2019) and morphometrically limits ingestible prey size (e.g. Piet et al. 1998, Scharf

et al. 2000). One explanation for this may be that in some species, the prey size spectrum becomes more variable with increasing predator size rather than showing a stable shift towards larger prey (Floeter & Temming 2003, Pinnegar et al. 2003). This phenomenon is corroborated by cod, with its intraspecific variation in prey preferences (Hüssy et al. 2016), driving the ordination of the predator trait maximum length. Furthermore, the high variability in prey types considered in the study raises the question of which maximum size should be considered to address a potential gape size limitation most appropriately. In cases of prey items with a large maximum body dimension but soft texture, the most prominent example being polychaetes, maximum length may be irrelevant when it comes to consumption by the predator. In future studies in which a diverse prey spectrum is considered, the role of prey size must therefore be addressed with a different trait, for example the maximum size of the smallest body dimension (i.e. the body diameter). Alternatively, a new trait combining size and texture or flexibility may be explored.

RLQ ordination suggested a gradient from piscivorous (greater sandeel, whiting) via more generalist (grey gurnard, cod) to benthivorous predators (haddock, plaice, dab) along the first axis. Since the method aims at an ordination that maximizes covariance (Dolédec et al. 1996, Dray et al. 2014), the absence of a link between predator traits and the traits of sandeels was likely due to their universal consumption by predators with different characteristics. The importance of distinctive prey types rather than common ones in this analysis would also explain why plaice, despite high sandeel proportions in its stomach, was located close to the benthivores haddock and common dab rather than close to the piscivores. Overall, the distribution of predators and prey types in the RLQ dimensions corresponded well with existing diet-based classifications of North Sea demersal fishes. The method added value by illustrating otherwise rather bin-like classifications (piscivorous, benthivorous, omnivorous) in a continuous, multidimensional trait space based on functional properties.

4.3. Limitations of the study and advice for future trait-based diet analyses

Trait information was drawn from pre-existing databases, literature and, in part, expert judgement, compiling one trait value per species. The representation of a species by a single trait value, however, negates intraspecific variation and, in some cases, may be lit-

tle informative for the system considered. The absence of a significant association between predator and prey size, for instance, might be the consequence of considering the fixed trait 'maximum length' rather than actual length measurements (which we would term 'state' as opposed to 'trait'). Analysing the state effect was not possible owing to the lack of prey size measurements in the stomach databases sourced for this study. Predator sizes, however, were in fact available and were much more homogeneous (mode of length between 20 and 45 cm across predator species) than species maximum body sizes sourced from the literature (between 40 and 140 cm). This discrepancy suggests an added value of actual state measurements, even though literature-based trait data compilation may be the only option for cost-effective trait analyses (e.g. Pecuchet et al. 2017, Beukhof et al. 2019b).

In the present study, data availability was higher for some traits (e.g. fish maximum length, Heessen et al. 2015) than for others (e.g. prey protection, mobility), and in general, data were more frequently available for fishes than for benthic invertebrates (e.g. energy density). Gaps in the trait tables thus had to be filled by adducing values measured for taxonomically closely related species, introducing a potential source of bias but at the same time being the best available proxies. Similarly, up-to-date measured data were not available for the traits omega-3 PUFAs and proteins, and instead were sourced from Hicks et al. (2019), who in turn refer to the FAO infood database (FAO 2016) as the source for the omega-3 PUFA contents of fishes. While we acknowledge that the FAO data are derived from conversion factors by Weihrauch et al. (1977), this was the only data source which provided consistent information across a wide range of species. In summary, the compilation of trait data was challenging for certain traits and species, and in some cases required the reliance on proxies and best available data sources. However, we are confident in the reliability of our method, because several known interactions are well-reflected in the results.

Lacking overlap of stomach content and benthic field data resulted in the decision to limit prey electivity studies to fish prey, only providing partial insight into prey preferences. Overlapping (infauna, epifauna, fish, stomach data) information was only available for grey gurnard sampled during a specific cruise on the Dogger Bank dedicated to cross-taxon sampling (Weinert et al. 2010, Sell & Kröncke 2013). Upscaling such cross-taxon sampling campaigns in the future would enable integral prey electivity analyses and deliver spatially and temporally corresponding

data sets that can give further insights into cross-taxon interactions and community shifts.

Sufficient data of reasonably high taxonomic resolution with regards to prey were available for only 7 predator species, even though we used the most comprehensive data set of fish stomach contents from the North Sea available. To capture interspecific, as well as (temporal and spatial) intraspecific variation in diets, systematic large-scale stomach data survey campaigns in the (southern) North Sea are required more regularly: the last one was the so-called ICES 'Year of the Stomach' 1991 (ICES 1997), and its data serve as the basis for North Sea food web models still in use today (Mackinson & Daskalov 2007, Stäbler et al. 2016, Püts et al. 2020, 2023). Since then, modern genetic methods have emerged, such as metabarcoding and eDNA analyses, which may be used complementary to classic stomach content analysis to enhance the taxonomic resolution of the prey consumed by North Sea fishes (Amundsen & Sánchez-Hernández 2019).

4.4. Conclusions and outlook

With current environmental changes and anthropogenic activities affecting marine ecosystems worldwide, reducing taxonomically complex food webs to their functional structure may help to improve our understanding of bottom-up and top-down processes and aid in estimating potential consequences of habitat change (e.g. Spitz et al. 2014, Gravel et al. 2016, Brose et al. 2019).

The methodological framework applied here was developed from a set of pre-existing analysis approaches. RLQ and fourth-corner analyses have been acknowledged as particularly rigourous methodologies for trait analysis (Beauchard et al. 2017), and have been improved and applied frequently over past decades, including for predator—prey trait analysis (Dolédec et al. 1996, Legendre et al. 1997, Tall et al. 2006, Dray & Legendre 2008, Dray et al. 2014, Spitz et al. 2014). Here, they were used for the first time to assess the feeding behaviour of the southern North Sea demersal fish community and proved to be suitable to link an observed pattern of feeding habits to an underlying functional explanation.

The findings concerning the role of omega-3 contents make this trait an interesting candidate for future functional diet studies. As a first step, however, species-specific omega-3 PUFAs and their temporal variability should be studied in more detail, applying appropriate methods for chemical analysis

(compare Graeve et al. 1994, Peters et al. 2015, F. Schäfer et al. unpubl.). The same is true for energy density, a trait known to show temporal variation (e.g. Zwarts & Wanink 1993, Pedersen & Hislop 2001), related to changes in food availability and behaviour (Hinz et al. 2005).

Prospectively, the outcomes of this and future trait-based analyses of feeding patterns may offer a promising basis for relating functionally similar predator species and their population dynamics to changes in their prey populations and potentially projecting these into the future. In practice, such an analysis could be performed with a food web model, with regards to the southern North Sea, for example, the already existing Ecopath with Ecosim (EwE) model (Stäbler et al. 2016, Püts et al. 2020, 2023), using the information on key traits to define functional groups within the model and cluster species accordingly.

Beyond that, a central advantage of trait-based analyses is the comparability across systems with varying species compositions (e.g. Mouillot et al. 2013, Beukhof et al. 2019c, Brose et al. 2019, McLean et al. 2021). With climate-change-driven species distribution shifts already occurring (Perry et al. 2005, Dulvy et al. 2008, Hiddink et al. 2015), knowledge of the functional profile of immigrating species can help to project their future role in the food web they are immigrating into, and the resulting implications for native species through competition and bottom-up or top-down pressures.

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