Fish functional groups of the North Atlantic and Arctic Oceans

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Abstract

International efforts to assess the status of marine ecosystems have been hampered by insufficient observations of food web interactions across many species, their various life stages, and geographic ranges. Hence, we collated data from multiple databases of fish stomach contents from samples taken across the North Atlantic and Arctic Oceans containing 944,129 stomach samples from larvae to adults, with 14,196 unique interactions between 227 predator species and 2158 prey taxa. We use these data to develop a data-driven, reproducible approach to classifying broad functional feeding guilds and then apply these to fish survey data from the Northeast Atlantic shelf seas to reveal spatial and temporal changes in ecosystem structure and functioning. In doing so, we construct individual predator-prey body~~- size~~ mass scaling models to predict the biomass of prey functional groups, e.g., zooplankton, benthos, and fish, for different predator species. These predictions provide empirical estimates of species- and size-specific feeding traits of fish, such as predator-prey mass ratios, individual prey mass, and the biomass contribution of different prey to predator diets. The functional groupings and feeding traits provided here help to further resolve our understanding of interactions within marine food webs and support the use of trait-based indicators in biodiversity assessments. The data used and predictions generated in this study are published on the Cefas Data Hub at: https://doi.org/10.14466/CefasDataHub.149 (Thompson et al., 2024).

Keywords: feeding guilds; species traits; marine ecosystem structure and functioning; food web indicator; biodiversity; trophic interactions; stomach contents data.

1 Introduction

Human pressures are affecting global patterns in marine ecosystem structure and functioning, from species distributions and their body sizes, to how and where energy fluxes through food webs (Daufresne et al., 2009; du Pontavice et al., 2020; Kortsch et al., 2015). Grouping organisms into broad functional feeding guilds and assessing change in their populations has been widely advocated to assess marine ecosystem status, gauge sustainable levels of human pressure, and inform management interventions (ICES, 2018; Rombouts et al., 2013; Tam et al., 2017). Yet, international efforts to develop indicators of marine ecosystem status have been hampered by the large number of observations needed to understand food web processes involving many species, their various life stages, and geographic ranges.

Despite the complexity of natural food webs, their structure and dynamics are largely determined by the size of the interacting organisms because predators are systematically larger than their prey, especially in aquatic ecosystems (Brose et al., 2006; Petchey et al., 2008; Woodward et al., 2005). The behaviour of organisms relating to their evolutionary history, including adaptations for specific foraging strategies and habitats, also affects predator-prey interactions (Brose et al., 2019; Link, 2004; Pecuchet et al., 2020; Pomeranz et al., 2019a). Fish fulfil many different roles in an ecosystem (Katara et al., 2021), often starting life as planktivores which feed lower in the food web, with some species developing into intermediate (e.g., benthivores) and higher predator feeding guilds (e.g., piscivores) which consume larger prey as they grow. Despite differing methods being used to classify ~~Fish~~ fish into feeding guilds, their biomasses ~~are also~~ have been shown to ~~responsive~~ respond to human pressures including fishing and climate change ~~-~~(Garrison & Link, 2000a, 2000b; Thompson et al., 2020). Analysing change in fish feeding guild biomass can, therefore, provide simultaneous information on ecosystem structure and functioning, by revealing temporal change in the spatial distribution of, e.g., planktivore biomass (structure) which is also indicative of change in energy flux between plankton and fish (functioning). Change in ~~feeding guild~~ the species richness of predators in feeding guilds provides a measure of functional redundancy where, for instance, relatively low and decreasing values highlight areas where a function is supported by only a few species and is at risk.

Internationally coordinated surveys with observations on fish species distributions, body sizes and biomass provide extensive data to assess change in fish feeding guilds (Lynam & Ribeiro, 2022). Complementing these, many fish stomach content data that contain information on food web interactions have been collected across the North Atlantic and Arctic Oceans (Arroyo et al., 2017; Cachera et al., 2017; ICES, 1997; Pinnegar, 2019; Smith & Link, 2010; Torres et al., 2013). However, idiosyncrasies in how feeding information has been quantified and reported across different stomach content databases have hampered efforts to depict general feeding traits. Specifically, four feeding guilds relevant to fish are used in OSPAR (The Convention for the Protection of the Marine Environment of the North-East Atlantic) and EU's MSFD (Marine Strategy Framework Directive) reporting processes, but without an agreed, data-driven method to categorise predators into them (i.e., planktivores, sub-apex demersal, sub-apex pelagic and apex predators; Boschetti et al., 2021; Walmsley et al., 2016~~ see also https://oap.ospar.org/en/resource-catalogue/enumeration-tables/cemp-enumeration-tables/~~). Any macroecological assessment of feeding guilds may therefore be confounded because changes could have a methodological basis. This has constrained the contribution of food web indicators to marine ecosystem status assessment.

The body~~- size~~ mass scaling relationship between individual predators and ~~their~~ individual prey (henceforth, predator-prey body-mass scaling) offers a means to depict general feeding traits across many species, their various life stages, and geographic ranges that have so far been lacking. Predator-prey body~~- size~~ mass scaling is also important to measure empirically because it can affect the pathway and quantity of energy flux through a food web (Barnes et al., 2010; Brose et al., 2019; Nakazawa et al., 2011; Schneider et al., 2012). Predators feeding on relatively small prey yield high predator-prey mass ratios (PPMR) that can dampen strong oscillatory dynamics ~~Predators feeding on relatively small prey with high predator-prey mass ratios (PPMR) can dampen strong oscillatory dynamics~~ and thus help to maintain stability in food webs (Otto et al., 2007; Rooney et al., 2006) and ecosystem functioning (Nakazawa et al., 2011; Schneider et al., 2012; Wang & Brose, 2018). Moreover, both predator and prey taxonomy and their traits can be used to predict interactions with typically high PPMRs that may be particularly important to conserve (Brose et al., 2019; Reum et al., 2019). For instance, we anticipate that planktivorous and benthivorous fish will have some of the highest PPMRs, especially those that remain in the same feeding guild through ontogeny, while fish species which develop into piscivores could see the largest change (a decrease) in their PPMR across their individual body ~~size~~ mass range.

Here we make use of predator-prey body~~-size~~ mass scaling relationships to draw on multiple stomach content databases and derive comparable fish feeding trait information for the North Atlantic and Arctic Oceans~~s~~. This new data collation contains observations from 944,129 fish stomachs collected between 1836 - 2020. We use these feeding traits to categorise fish into feeding guilds in a way that is conducive to their application internationally, across ecosystems. Feeding guilds are then applied to survey data collected from across the northeast Atlantic shelf seas to demonstrate macroecological patterns in ecosystem structure and functioning relevant to status assessment advocated by OSPAR. We test the following hypotheses: i) intra and interspecific body~~-size~~ mass scaling for predator species is dependent on prey group (e.g., plankton, benthos, and fish prey); ii) multiple distinct feeding guilds are evident based on feeding trait data; iii) the effectiveness to reliably and robustly classify predators into feeding guilds applicable across ecosystems varies due to whether classifications are based on the biomass of prey taxa, prey taxa occurrence, or broad feeding traits (i.e. PPMR, mean prey body-mass, and the % biomass contribution of different prey functional groups); iv) feeding guilds capture significant spatio-temporal trends in survey data. Our aim was twofold: to generate empirical estimates of fish feeding traits that could help improve understanding of changes in marine ecosystem structure and functioning; and to achieve international consensus on the best approach to assessing feeding guilds across ecosystems within the OSPAR Maritime Area and in a way that can be readily extended to other areas (e.g., n~~N~~ortheast US continental shelf where applicable and routinely collected survey data exist but were outside the scope of our assessment) and organisms (e.g., invertebrates and mammals).

2 Methods

2.1 Stomach contents data

We draw together stomach contents data primarily collected from the North Atlantic shelf seas, with important contributions from the Baltic, Barents and Norwegian Seas (Fig. 1, S1). These data were sourced from a combination of previously published and unpublished data including DAPSTOM (An Integrated Database & Portal for Fish Stomach Records; Pinnegar, 2019), ICES Year of the Stomach (Daan, 1981; ICES, 1997), the Northeast US continental shelf (Smith & Link, 2010), Northern Spanish shelf (Arroyo et al., 2017), Gulf of Cadiz (Torres et al., 2013), Swedish-, Icelandic-, Norwegian-, French- (Cachera et al., 2017; Timmerman et al., 2020; Travers-Trolet, 2017; Verin, 2018) and German-led surveys (e.g., FishNet, https://www.nationalpark-wattenmeer.de/wissensbeitrag/fishnet/). We have included stomach contents data from outside the OSPAR Area (i.e., Northeast US continental shelf and Baltic Sea) to demonstrate the wider applicability of our approach to defining feeding guilds and because those data have been used to classify feeding guilds previously (Garrison & Link, 2000a). The full data collation contains observations from larval~~e (<1 g)~~ to adult predators~~s~~ (i.e. fish whose stomach contents have been sampled, ranging from ~~up to~~<1g to 351 kg), representing 14,196 unique interactions between 227 predator species and 2158 prey taxa (i.e., prey are defined as organisms found in stomach contents; https://doi.org/10.14466/CefasDataHub.149; Thompson et al., 2024). We provide a summary of data sources, spatial and temporal ranges, and sample distributions in Table 1. All data processing and subsequent analyses were conducted in R version 4.02 (R Core Team, 2020). Predator and prey taxonomy were processed using the “taxize” package (Chamberlain et al., 2020)

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and assigned to 'zooplankton', 'benthos', 'fish', 'nekton' and 'other' functional groups after Webb & Vanhoorne (2020) using the "worrms" package (Chamberlain, 2019).

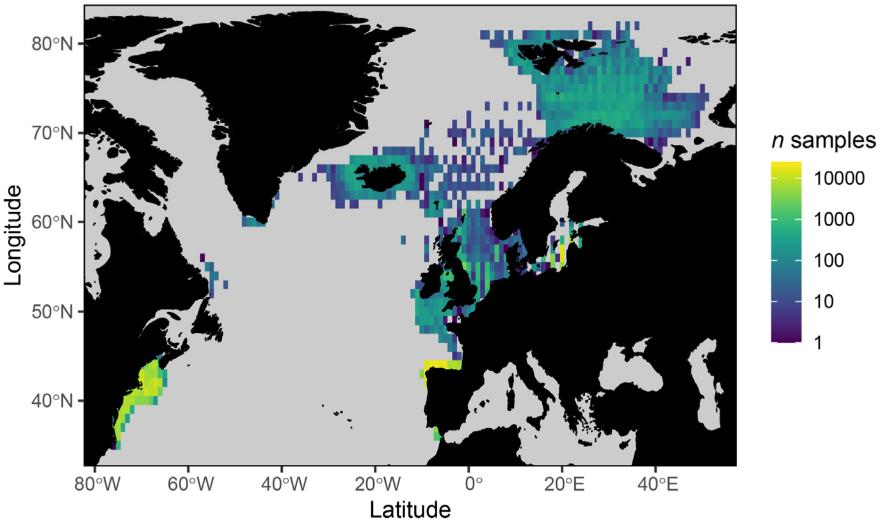

Figure 1: Number of stomach samples on a 1° longitudinal by 1° latitudinal grid.

Table 1. A summary of data sources, spatial and temporal ranges, and sample distributions (see also Fig. S1).

Source	**Temporal range**	**Latitudinal range**	**Longitudinal range**	***n* stomachs**	***n* predator taxa**	***n* prey taxa**
DAPSTOM	1836 to 2016	44 to 80	-57 to 50	89500	113	838
France	2009 to 2018	49 to 51	-2 to 2	895	16	254
Germany	2019 to 2020	54 to 55	8 to 9	312	21	67
Iceland	1992 to 1992	63 to 67	-27 to -10	32744	22	506
ICES - Baltic	1963 to 2014	54 to 60	10 to 24	66829	1	124
ICES - North Sea	1980 to 2013	51 to 62	-6 to 12	251006	29	781
Norway	2004 to 2020	69 to 82	-9 to 51	56406	3	348
Spain	1988 to 2019	36 to 44	-10 to -1	181494	97	354
Sweden	2013 to 2013	56 to 59	8 to 13	268	1	52
USA	1973 to 2019	35 to 45	-76 to -65	264675	58	258

2.2 Quantifying intra- and interspecific body~~- size~~ mass scaling relationships between predators and different prey functional groups

Prey count and biomass observations (wet weight in grams) are needed to estimate predator-prey mass ratios (PPMR), but these were available for only 56% of the stomach contents data. Therefore, to make use of all the data (Fig. 1; Table 1) when assigning fish to feeding guilds, a linear mixed effect model of predator-prey body~~- size~~ mass scaling was constructed to estimate prey counts or biomass where either were unavailable; using only data where taxonomy for both predator and prey was resolved (i.e., to species and functional group, respectively), and individual predator body ~~size~~mass, individual prey body ~~size~~ mass and prey counts were all available. Major axis regression following Brose *et al.* (2019) was not suitable because we needed to make predictions of individual prey body ~~size~~ mass and minimise the squared residuals in the response (Legendre, 1998). Log10-transformed individual prey mass (wet weight in g) was modelled as the response variable, with log10-transformed predator body mass (wet weight in g) as a fixed effect. Random intercepts and slopes were included for predator taxa and prey functional group to account for potential variation in their relationships with predator body mass. Random intercepts were fit for datasets which follow different protocols to test for systematic differences in how data were generated (i.e. Spain, USA, and ICES, which each follow their own protocols for measuring prey biomass, and all others which represent a mixture of methods from across studies). Random intercepts were also fit for years, sites (Fig S1; sites based on a 3 by 3 grid across the study region) and the number of stomachs sampled (i.e. 1 = from multiple stomachs and 2 = where stomach samples were pooled). We use a Student's t-distribution to account for heavy tails in the distribution of the response. We use the following model: ~~Log$_{10}$ transformed individual prey mass (wet weight in g) was fit as the response, with an interaction term between log$_{10}$ transformed predator body mass (wet weight in g). Random intercepts and slopes were fit for both predator taxa or prey functional group to test if either interacted with predator body mass. Random intercepts were fit for datasets to test for systematic differences in how data were generated: grouped into those from Spain, USA, and ICES, which each follow their own protocols for measuring prey~~

~~biomass, and all others which represent a mixture of methods from across studies. Random intercepts were also fit for years, sites (a 3 by 3 grid across the study area based on splitting the gradients of longitude and latitude into 3 equal lengths; Fig S1) and the number of stomachs sampled with two levels, 1 = from multiple stomachs and 2 = were stomach samples were pooled (some stomach samples contained in DAPSTOM and ICES Year of the Stomach were pooled at the point of collection for size classes of predator species). We use a Student's t-distribution to account for heavy tails in the distribution of the response.~~

$$\mathrm{Log10}(\text{prey mass})_i \sim Student - t\left(\alpha_{j[i],k[i],l[i],m[i],n[i],o[i]} + \beta_{1j[i],k[i]}(\text{predator mass}), \sigma^2, \mathrm{v}\right)$$

$$\begin{pmatrix} \alpha_j \\ \beta_{1j} \end{pmatrix} \sim N\left(\begin{pmatrix} \mu_{\alpha_j} \\ \mu_{\beta_{1j}} \end{pmatrix}, \begin{pmatrix} \sigma^2_{\alpha_j} & \rho_{\alpha_j \beta_{1j}} \\ \rho_{\beta_{1j}\alpha_j} & \sigma^2_{\beta_{1j}} \end{pmatrix}\right), \text{ for predator\_taxa j = 1, … ,J}$$

$$\begin{pmatrix} \alpha_k \\ \beta_{1k} \end{pmatrix} \sim N\left(\begin{pmatrix} \mu_{\alpha_k} \\ \mu_{\beta_{1k}} \end{pmatrix}, \begin{pmatrix} \sigma^2_{\alpha_k} & \rho_{\alpha_k \beta_{1k}} \\ \rho_{\beta_{1k}\alpha_k} & \sigma^2_{\beta_{1k}} \end{pmatrix}\right), \text{ for prey\_functional\_group k = 1, … ,K}$$

$$\alpha_l \sim N\left(\mu_{\alpha_l}, \sigma^2_{\alpha_l}\right), \text{ for year l = 1, … ,L}$$

$$\alpha_m \sim N\left(\mu_{\alpha_m}, \sigma^2_{\alpha_m}\right), \text{ for data source m = 1, … ,M}$$

$$\alpha_n \sim N\left(\mu_{\alpha_n}, \sigma^2_{\alpha_n}\right), \text{ for site n = 1, … ,N}$$

$$\alpha_o \sim N\left(\mu_{\alpha_o}, \sigma^2_{\alpha_o}\right), \text{ for } n \text{ stomachs pooled o = 1, … ,O}$$

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Where Log_{10} transformed individual prey mass (wet weight in g) is modelled following a Student's t-distribution with mean μ, variance σ^2, and degrees of freedom v. The parameters α and β represent intercepts and slopes, respectively, that vary by grouping factors j to o. The Akaike Information Criterion (AIC) was used on nested models to assess the importance of all predictors. The full model had the lowest AIC by >2 units meaning all predictors were retained (Table S1). Model diagnostic plots were performed using the R package *DHARMa* (Hartig, 2022).

The 'full' model was used to predict the mean individual body mass of prey functional groups for predator species of a given size. This enabled us to make use of many observations in DAPSTOM, for instance, which have recorded prey counts but no prey biomass. In such cases, we estimated the biomass of each prey taxa by multiplying the predicted mean individual body mass for their functional group by the observed prey count. Where prey counts were missing, e.g., much of the data from Smith & Link (2010; USA data in Fig. S1), we estimate these by dividing the observed biomass of each prey taxa by the predicted mean individual prey mass for their functional group. We provide R script and the data underlying our model, with an example showing how to predict mean individual prey size (i.e. generate fitted values) based on a list of predator taxa, predator body mass and prey functional groups (https://github.com/MurraySAThompson/fish-feeding-traits-glmm). Here we also demonstrate how to simulate data using the uncertainty measured by our model to help gauge its performance and because variability in individual prey masses is useful in food web research more broadly (Brose et al., 2019; Pomeranz et al., 2019b; Scott et al., 2014)~~based on a list of predator taxa, predator sizes and prey functional groups (https://github.com/MurraySAThompson/fish-feeding-traits-glmm)~~. Our full model has temporal and spatial information as random effects because we were interested in developing general feeding traits for the study area, irrespective of spatial and temporal gradients. However, the significance of spatial and temporal random effects (Table S1) suggests future work exploring environmental change drivers of predator-prey body-mass scaling could be fruitful. All linear mixed effects models were fit using the *glmmTMB* R package (Brooks et al., 2017).

2.3 Classifying predator feeding guilds based on feeding trait data

Predators were categorised by species and ~~size~~individual body mass. We use 20 equal size bins to categorise predator mass along a $\log_{10}$ transformed gradient from 0.1 micrograms to 190 tonnes, capable of capturing organisms from plankton to blue whales (Table S2). Data for each species grouped into body mass bins~~size class~~ (henceforth species body-mass bins) was then estimated across all available stomach samples (Fig. 1; Table 1), with means calculated for % prey functional group biomass, biomass weighted PPMR (after Reum et al., 2019) and mean individual prey mass (see feeding guilds.csv; https://doi.org/10.14466/CefasDataHub.149)~~Table S3)~~. We used directly observed data where available and predictions (i.e. the fitted values) from our predator-prey body~~- size~~ mass scaling models where data were missing. Feeding guilds were assigned based on cluster analysis using the 'ward D2' agglomeration method on Bray-Curtis dissimilarities between predator diets available in the R *stats* package (R Core Team, 2020).

We compared different methods to classifying feeding guilds where the dissimilarity matrix used in the cluster analysis was generated using either: 1) the biomass of prey taxa (Garrison & Link, 2000a); 2) prey taxa occurrence (Thompson et al., 2020) or; 3) via a novel method where dissimilarities are based on broad feeding traits (henceforth, the biomass, occurrence and trait methods). Feeding traits were $\log_{10}$ transformed mean individual prey mass (g), $\log_{10}$ transformed mean biomass weighted PPMR, and the mean % biomass contribution to the stomach contents of zooplankton (including fish <0.5g), benthos, nekton (other than fish) and fish (all fish prey ≥ 0.5g); with all variables rescaled to values of or between 0 and 1. We tested for differences between these methods to classifying feeding guilds by comparing them after re-sampling (*n* = 1000) subsets of the data (*n* = 30 unique stomach samples per predator). Predators with fewer than 30 samples were not classified into feeding guilds. Compositional change in predators between successively reclassified feeding guilds was used to determine the ability of each method to consistently classify similar predators in the same guild. Compositional change was measured using the distance to centroid following analysis of multivariate homogeneity of groups dispersions (Anderson, 2006). The method with the lowest mean distance to centroid was determined to have the most robust feeding guild classifications as determined using analysis of variance tests. First, we tested whether compositional change across feeding guilds was non-random for each method: distance to centroid (i.e., compositional change) was the response, with 'Guild', and 'Data' (i.e., a factor identifying each unique re-sampling event) as predictors. We then tested for significant differences between methods: distance to centroid (i.e., compositional change) was the response, with 'Method', 'Guild', and 'Data' as predictors. Significant predictors were determined using the *F*-test on nested models. Targeted tests for differences between the mean distance to centroid across methods were carried out using Tukey's all-pairwise comparisons that corrects for multiple comparisons in the "multcomp" package (Hothorn et al., 2016).

The ability to classify common feeding guilds across ecosystems (e.g., sub-apex and apex predators) rather than area-specific guilds (e.g., a feeding guild unique to the North Sea) is another important quality for a feeding guild indicator to exhibit. We assessed how important spatial gradients were in our three different approaches to classifying feeding guilds. First, we generated latitudinal and longitudinal coordinate centroids for each predator by taking a mean across their stomach samples. We then took a mean across these predator centroids to generate a centroid for all the data, and also means across these predator centroids but grouped by feeding guild and method to generate method-specific guild centroids. Next, we measured the distance between the overall data centroid to the method-specific guild centroids using the *geosphere* package (Hijmans et al., 2021) and summed distances for each method. A large sum of distances for a method to the overall data centroid would indicate that feeding guilds were area-specific, largely made up of predators found close together, and thus spatial gradients would be important determinants of feeding guild structure. The method with the lowest sum of distances to the overall data centroid was deemed to be least affected by spatial gradients and thus preferred.

We provide a sensitivity analysis for whether our modelled stomach contents data affected our conclusions about which approach to feeding guild classification was optimal. Using only observed data for prey weight and counts from DAPSTOM, ICES Year of the Stomach and data from the Northeast US continental shelf (i.e. those that have published prey taxa information), we compare the ability of the different approaches to consistently classify similar predators in the same guild and classify common feeding guilds across ecosystems, as described above. Results are provided in the Supporting Material.

Four feeding guilds have been called for in OSPAR and MSFD guidance, i.e., planktivores, sub-apex demersal, sub-apex pelagic and apex predators (Boschetti et al., 2021; Walmsley et al., 2016; see also https://oap.ospar.org/en/resource-catalogue/enumeration-tables/cemp-enumeration-tables/), without consensus on how to categorise predators into these guilds. We use four feeding guilds here to help bridge this gap and so that we can elegantly capture a broad set of ecosystem components while exploring guild responses in biomass and species richness in the survey data. Changing the number of feeding guilds could be justified, depending on the question, and is straightforward to implement by taking a higher or lower split in the classification tree. We see this as a strength of our approach because feeding guilds are hierarchically structured much like how taxonomic or other trait information has been organised. We provide a table which details the branches for up to five feeding guilds so future assessments can choose which level of complexity suits their need. We also present axis scores from a non-metric multidimensional scaling analysis of the dissimilarities used in our cluster analysis which provide a more nuanced understanding (i.e., bounded data as opposed to categorical) of different predator feeding traits in relation to others. Moreover, because it is a data-driven, reproducible approach, new information can be systematically integrated to 1) further resolve differences in feeding traits, 2) feeding guild composition and 3) test if changes in predator feeding traits provides evidence for spatially or temporally flexible classifications.

2.4 Using feeding guilds to capture spatiotemporal trends in survey data

The new feeding guild classifications have been applied to processed otter trawl survey data for the Northeast Atlantic shelf seas collected between 1997–2020 (Lynam & Ribeiro, 2022) to reveal spatial and temporal patterns in feeding guild responses (Fig. 2). These survey data have been processed specifically to support state indicators, with observations for the biomass of species body-mass bins ~~species size classes~~ standardised to the area swept for each haul. Survey data corresponding with all our stomach content data, from north of Norway, Icelandic waters, the Baltic Sea and eastern shelf seas of the USA, have not yet been standardised and processed in the same way, hence why we haven't included them here. Extending this work to assess change in ecosystem structure and function across the study region covered by the stomach contents data (Fig. 1) represents a key area for future development. We also provide the necessary R code (https://github.com/MurraySAThompson/fish-feeding-guild-classifcation) so that our feeding guilds can be readily appended to new survey data when available and processed as required.

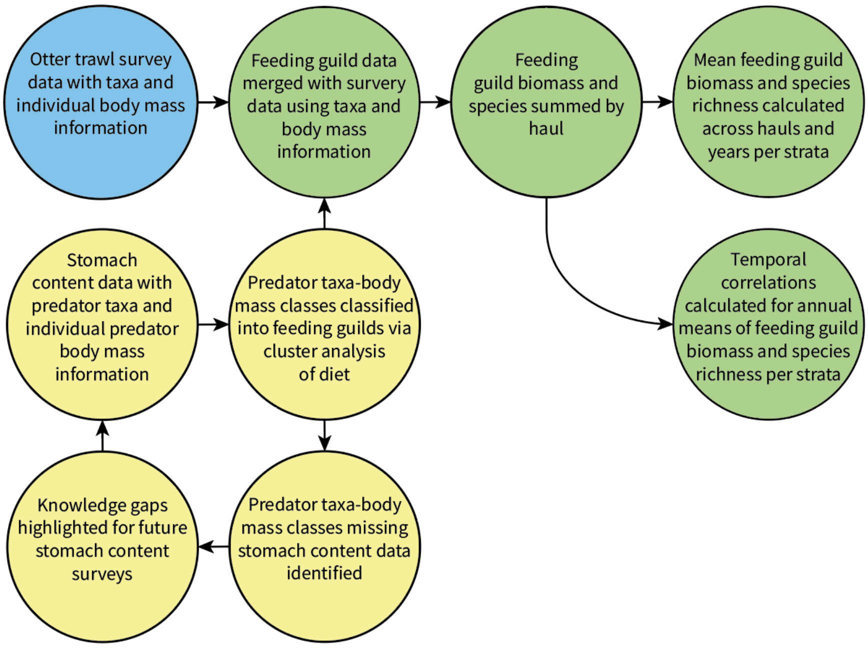
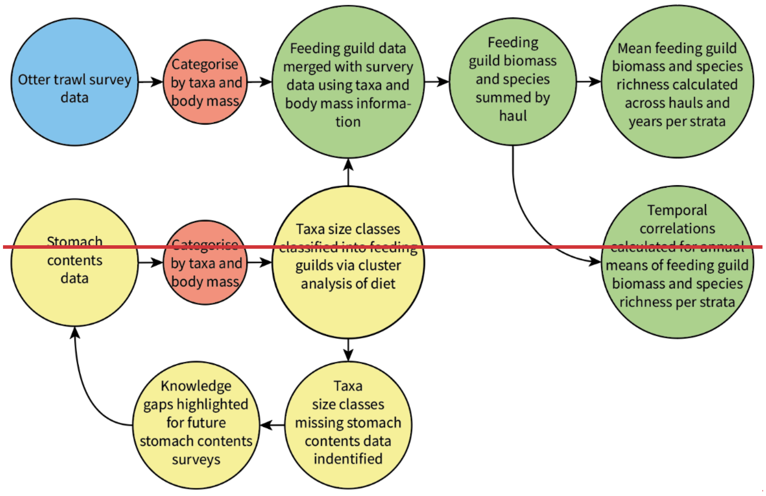


Figure 2: The process used to classify feeding guilds based on predator stomach contents data, assign them to survey data and calculate feeding guild responses across the assessment strata. Yellow circles = stomach contents data, blue circle = otter trawl survey data, green circles = survey data with feeding guild information appended, arrows = flow of information.

Compared with quarter 2 and 3 (April – September), data from quarters 1 and 4 (January-March and October – December, respectively) typically have longer time-series available over much of the study region and so were preferentially selected. Where data from quarters 1 or 4 were not available, otter trawl data from other quarters were used. Table S3~~4~~ provides information on the surveys used and their spatial and temporal ranges and Figure S2 depicts survey locations within OSPAR regions (e.g., Celtic Sea, North Sea). The temporal assessment covers 1997-2020 because the majority of the surveys considered have at least a near complete time-series covering that period. Longer time-series do exist for some surveys but including these data would mean we are looking at long-term change for some areas, but shorter-term change for others which could confound interpretation. Spatial and temporal change in feeding guild responses were determined for the Greater North Sea, Celtic Seas, Bay of Biscay and Iberian Coast, and the wider Atlantic. The assessment strata used here replicate those used for the OSPAR food web indicators: mean-maximum length and size-composition in fish communities (Lynam et al., 2022; Lynam & Piet, 2022).

Kendall's τ trend analysis was used to identify areas of significant temporal change in feeding guild responses based on the relationship between mean haul-level values of feeding biomass and species richness for each assessment strata and year. Kendall's τ scores of –1 to +1 represent a 100% probability of a decreasing or increasing trend, respectively. By using Kendall's τ, which is rank-based and non-parametric, we can detect correlations which may be non-linear. Stomach contents data, prey size predictions, haul-level estimates of feeding guild biomass and their species richness along with Kendall's τ correlation coefficients and *p* have all been made available (https://doi.org/10.14466/CefasDataHub.149; Thompson et al., 2024).



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3 Results

3.1 Unique intra- and interspecific individual body~~- size ~~mass scaling relationships between predators and prey functional groups

There were significant differences in the predator-prey body-mass scaling relationships between the different combinations of predators and prey functional groups (Fig. 3). ~~There were significant differences in the log$_{10}$ transformed scaling relationship between predator and prey body mass captured by the interactions between predator body mass and predator species and prey functional group combinations (Fig. 3). ~~These results support our first hypothesis that predator species can have unique intra- and interspecific body~~- size ~~mass scaling relationships with different prey functional groups. Fish prey tended to be the biggest, meaning fish-fish interactions tended to have higher intercepts and slopes (Fig. ~~3a~~3m, lines a, c, d, and h) and thus the lowest mean PPMR, with predator species of the same size consuming relatively small benthic and zooplankton prey (Fig. 3m, lines b, e, f, g, I, j, k, l). These models enabled us to estimate prey biomass, counts and predator-prey mass ratios across the different stomach contents datasets and ~~,~~ species body-mass bins~~species and size classes~~ useful for feeding guild classifications~~ (Table S3)~~.

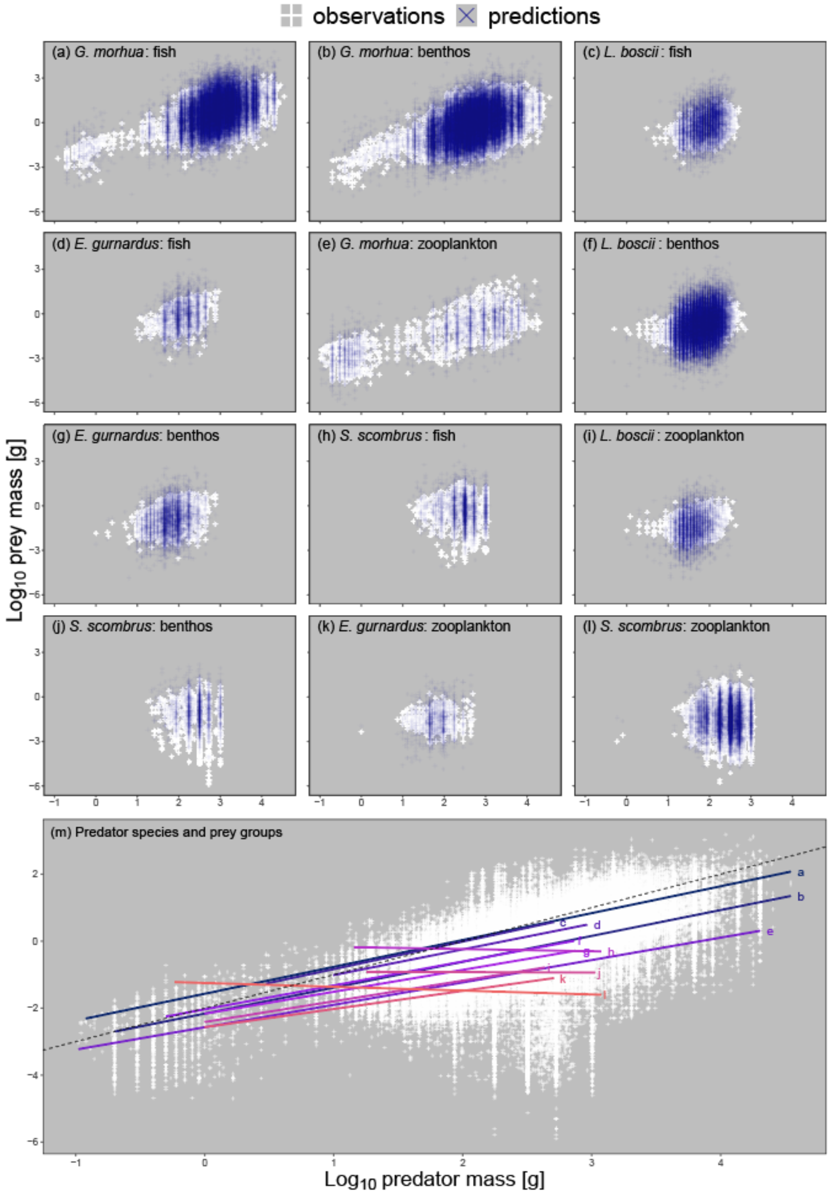

Figure 3. Panels a-l: ~~A~~ a subset of the 498 unique combinations of predator species and prey functional group ~~body mass scaling~~body-mass scaling ~~-~~relationships on log$_{10}$ transformed axes ordered from largest to smallest by prey mass at maximum predator mass. Predator individual body mass was fit as the predictor of prey individual body mass in our model, hence appearing on the x- and y-axes, respectively. We selected this subset because they represent important predators of fish, benthos and zooplankton across ecosystems (see https://github.com/MurraySAThompson/fish-feeding-traits-

glmm~~.~~ for R script to reproduce any unique predator species and prey functional group combination). ~~Blue~~ White points = observed values for specific relationships, ~~red~~ blue points = model predictions for specific relationships~~, grey points = all observed values~~. ~~The final plot 'Predator species and prey groups'~~Panel m: ~~shows~~ the different scaling relationships across the preceding plots~~, ordered by prey size at maximum predator size~~ with all observations (white points) and a dashed 1:1 line to show scaling relationships were generally sublinear (i.e., prey increased less than their predators per unit increase in individual body ~~size~~mass).

3.2 Feeding trait data reveal multiple distinct feeding guilds

Feeding guilds captured significant variation in the composition of predators for each cluster-based method (Table 2), confirming our second hypothesis that multiple feeding guilds can be delineated from the analysis of feeding traits. The occurrence method had the most robust feeding guilds with the lowest compositional change in predators following re-sampling (mean distance to centroid = 0.13), followed by the trait (mean distance to centroid = 0.22) and then the biomass methods (mean distance to centroid = 0.34; randomly generated feeding guild mean distance to centroid ranged between 0.6 – 0.61; Fig. S3~~2~~; Table S4~~5~~). The trait method had the lowest sum of distances to the data centroid (2,655 km) followed by the biomass (7,034 km) and occurrence methods (8757 km; Fig. ~~S3~~S4). The trait method was therefore preferred because it could identify multiple distinct feeding guilds even where we consider small subsets of predator stomach contents (*n* = 30 stomach samples) while being the least affected by spatial gradients in prey taxa composition. These results also confirm our third hypothesis that the effectiveness to reliably and robustly classify predators into feeding guilds applicable across ecosystems varies due to whether classifications are based on the biomass of prey taxa, prey taxa occurrence, or broad feeding traits. Results from our sensitivity analysis using only directly observed prey count and weight information reveals that the trait approach had both the most robust feeding guilds and lowest sum of distances to the data centroid, providing further support for our decision to use it to assess change in survey data (Table S4; Fi. S3).

The four feeding guilds identified using the trait method have been named based on the % biomass of prey functional groups as follows: planktivores, benthivores, bentho-piscivores and piscivores (Fig. 4). Differences between feeding guilds were related to predator size, which correlated positively with piscivory and negatively with planktivory (Fig. S5~~4~~). Small ~~size classes~~body-mass classes of species often occur in the planktivore guild, moving to another guild as they increase in size, with multiple medium- to larger ~~size~~body-mass ~~-~~classes of a species often in the same guild (~~Table S3~~see feeding guilds.csv; https://doi.org/10.14466/CefasDataHub.149). Typically, the biggest fish within and across feeding guilds had the highest PPMR (hence the sublinear relationship in Fig. 3 m, where prey increased less than their predators per unit increase in individual body ~~size~~mass), yet piscivores were typically the biggest and had the lowest PPMR on average. This apparent contradiction is largely because small piscivores had some of the lowest PPMR values, whereas big planktivores and benthivores had some of the highest values (Fig. 4~~; Table S3~~).

Table 2. Analysis of variance results across nested models for each cluster-based method and across methods. Data for biomass, occurrence and trait methods were used to test whether guild (i.e., cluster-based groups) and data (i.e., a factor identifying each unique re-sampling event) captured significant variation in the composition of predators. Data for all ~~was ~~were used to test for differences between the different methods (see also Table S4~~5~~; Fig. ~~S2~~S3). The term dropped column indicates which term was dropped from each model (blanks indicate no predictors were dropped), AIC reveals change in model fit, and *p*-values from *F*-tests highlight significant change in model fit.

Data	Term dropped	Df	AIC	*F*-value	*p*
Biomass			-19197		
	Guild	3	-18942	67.42	<0.001
	Data	999	-19400	1.7	<0.001
Occurrence			-16383		
	Guild	3	-14526	592.83	<0.001
	Data	999	-15784	2.74	<0.001
Trait			-~~16383~~20261		
	Guild	3	-~~14526~~14129	~~592.83~~3634.91	<0.001

	Data	999	-~~15784~~20505	~~2.74~~1.65	<0.001
All	<none>		-48990		
	Guild	3	-47509	483.29	<0.001
	Method	2	-43609	3113.44	<0.001
	Data	999	-49756	1.19	<0.001

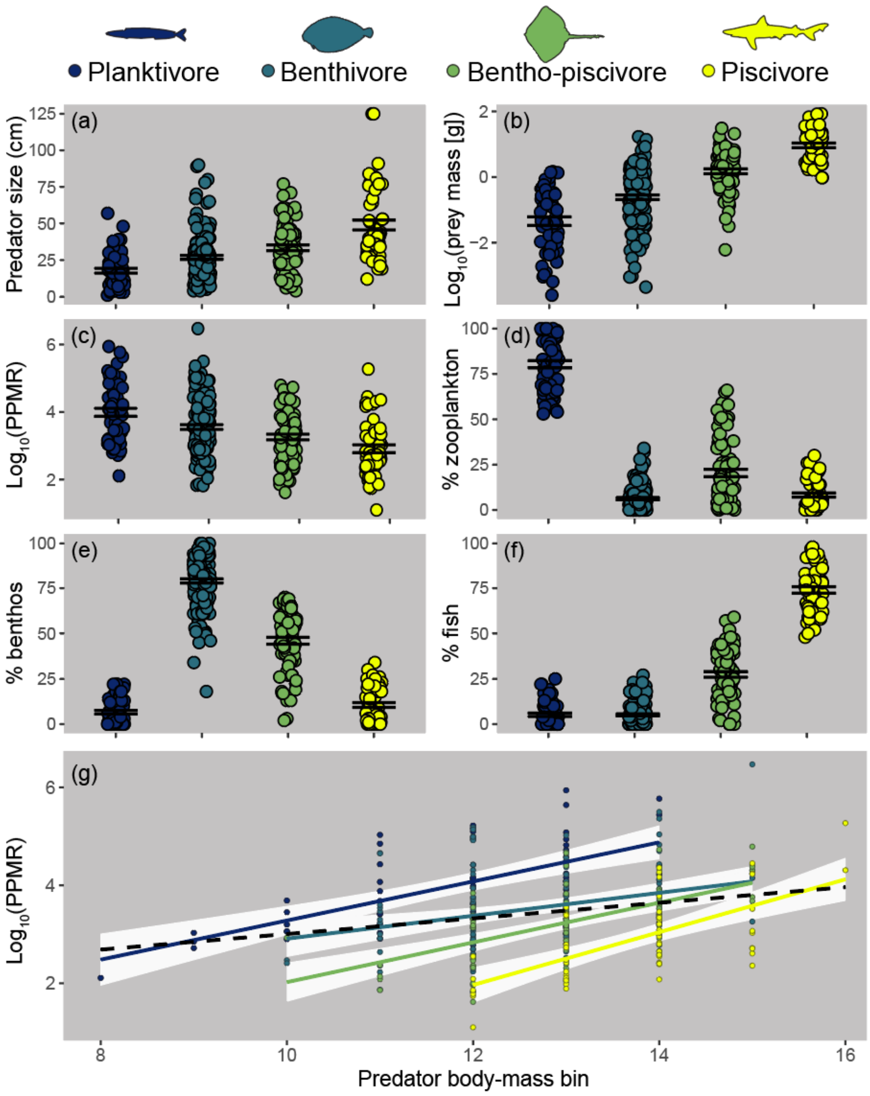

Figure 4: Differences between feeding guilds in predator size (a), individual prey ~~size~~mass (b), predator-prey mass ratio (PPMR; c) and the % biomass contribution of ~~different prey functional~~

~~groups~~zooplankton (d), benthos (e), and fish (f) to predator stomach contents. Points represent means for predator species ~~size classes~~body-mass bins~~ (Table S3)~~, error bars represent standard error. ~~Bottom p~~Panel g: PPMR increases with predator individual body ~~size~~ mass within (solid, coloured) and across (black, dashed line) feeding guilds.

3.3 Feeding guilds capture significant spatiotemporal trends in survey data

When assigning feeding guilds in the survey data, we were able to classify 92% of the biomass which included 122 species body-mass bins~~species size classes~~. Many rare predators observed in the survey data (*n* = 366, representing 8% of the surveyed biomass) remain unclassified due to insufficient stomach contents data (Table S5~~6~~). The perspective of change in the survey data is therefore weighted towards predators contributing most to community biomass and ecosystem functioning. We found clear spatial structure and regions of contrasting temporal change in feeding guild biomasses and their species richness (Figs. 5-6), confirming our ~~third~~ fourth hypothesis. For instance, significant and spatially extensive temporal decreases in planktivore feeding guild biomass (i.e., lower in the food web) ~~lower in the food web~~ were evident in the Celtic Seas and Bay of Biscay where the biomass of the bentho-piscivore and piscivore feeding guilds (i.e., higher in the food web)~~higher in the food web~~ has increased (Fig. 5). Benthivore biomass has increased in the southern North Sea, where there has been little change in other feeding guilds. Planktivore, bentho-piscivore and piscivore biomass have all decreased in at least one assessment strata in the northern North Sea. Regions of temporal change in species richness were also different across feeding guilds (Fig. 6). For instance, over large areas in the Celtic Seas, Bay of Biscay and northern North Sea where there was relatively limited change in planktivore species richness, the species richness of benthivores, bentho-piscivores and piscivores all increased (see Fig. S6~~5~~ for changes in unclassified biomass).

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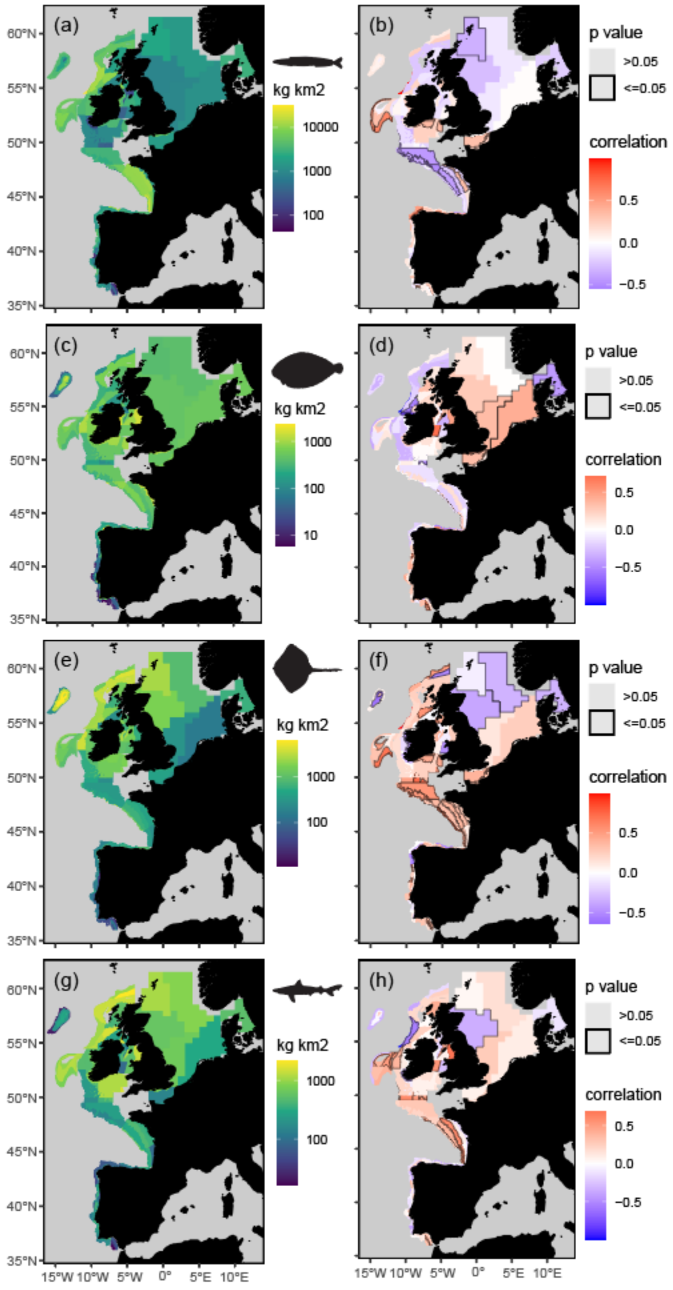

Figure 5: Mean spatial distribution (~~top row~~a, c, e, g) and temporal change (~~bottom row~~b, d, f, h) in feeding guild biomass by assessment strata based on otter trawl data for planktivores (a, b), benthivores (c, d), bentho-piscivores (e, f), and piscivores (g, h). Significant temporal trends are highlighted with a black border and coloured blue or red to depict a decreasing or increasing trend, respectively (Kendall's τ scores of −1 to +1 represent a 100% probability of a decreasing or increasing trend).

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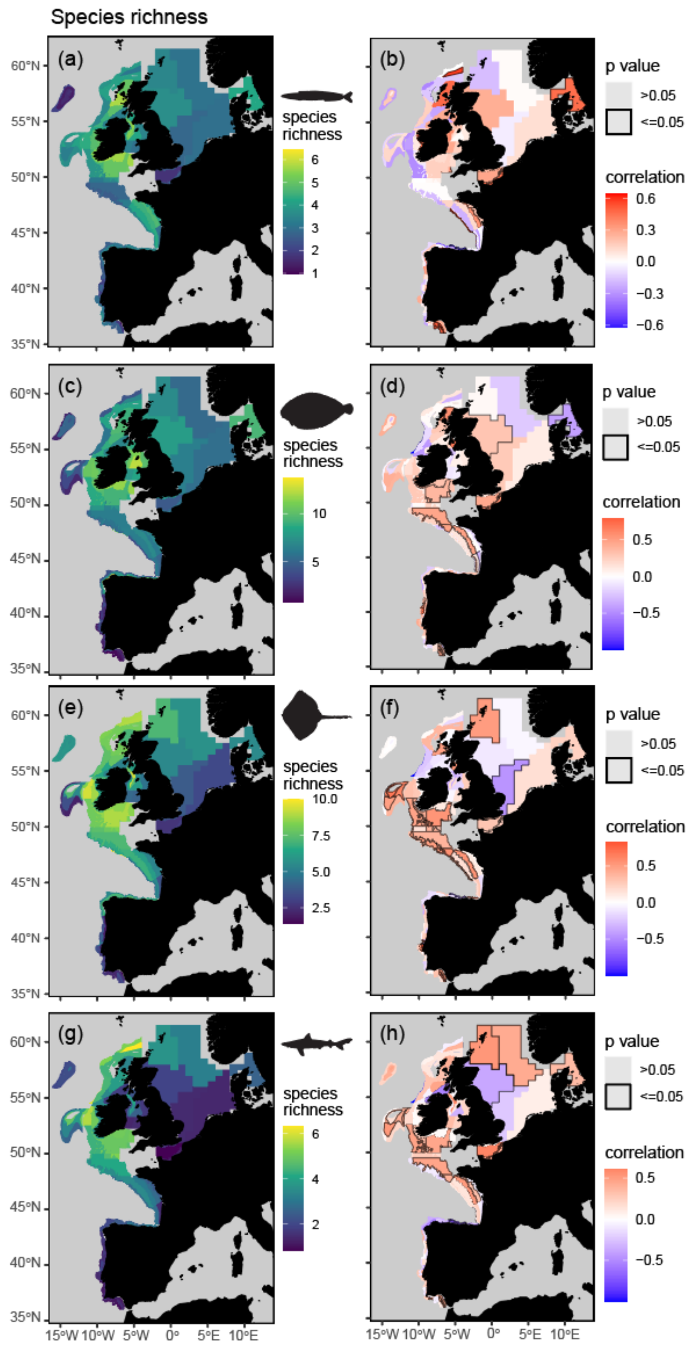

Figure 6: Mean spatial distribution (a, c, e, g) and temporal change (b, d, f, h) in feeding guild species richness by assessment strata based on otter trawl data for planktivores (a, b), benthivores (c, d), bentho-piscivores (e, f), and piscivores (g, h). Significant temporal trends are highlighted with a black border and coloured blue or red to depict a decreasing or increasing trend, respectively (Kendall's τ scores of −1 to +1 represent a 100% probability of a decreasing or increasing trend). ~~Mean spatial distribution (top row) and temporal change (bottom row) in feeding guild species richness by assessment strata based on otter trawl data. Significant temporal trends are highlighted with a black border and coloured blue or red to depict a decreasing or increasing trend, respectively (Kendall's τ scores~~

~~of –1 to +1 represent a 100% probability of a decreasing or increasing trend).~~

4 Discussion

Our predator-prey body-~~-size~~ mass scaling models enabled predictions of mean individual prey mass for different predator species and prey functional groups across the North Atlantic and Arctic Ocean's shelf seas~~s~~. With these predictions we could estimate key fish feeding traits across species and sizes, such as predator-prey mass ratios and the relative biomass contribution of zooplankton, benthos and fish prey to predator diets. Our feeding trait-based approach to categorising feeding guilds was also less susceptible to large spatial gradients in the composition of prey than previously used methods (Garrison & Link, 2000a; Thompson et al., 2020). By using feeding guilds to assess routinely collected survey data, we revealed contrasting patterns of change in the biomass and species richness of fish feeding at different levels within the food web across the Northeast Atlantic shelf seas. For example, extensive decreases in the biomass of consumers lower in the food web (planktivores) were evident in the Celtic Seas and Bay of Biscay and this contrasted with biomass increases higher up (bentho-piscivores and piscivores; Fig 5). These contrasting patterns of change in how biomass and species are distributed across the food web indicate regions of temporal change in marine ecosystem structure and functioning as the relative importance of different energy pathways changes across the fish assemblage. This is because changes in species richness and the distribution of biomass across the food web can influence nutrient uptake and the efficiency of communities in converting nutritional resources into biomass (Cardinale et al., 2012; Wang & Brose, 2018; Worm et al., 2006).

A wide range of prey sizes could be consumed by a given predator species and size and this variability was generally captured well by our models (Fig. 3). Omnivory was also ubiquitous with all prey groups occurring in the diet of all feeding guilds, albeit to markedly different levels (Fig. 4~~; Table S3~~). This, along with the variability in our re-sampled feeding guild classifications (Fig. S2), highlights the plasticity of fish feeding behaviour with some individuals of, e.g., a typically planktivorous species having consumed mostly fish prey. Feeding guilds provide a necessary simplification of this complexity as a means to indicate change in marine food webs across ecosystems by taking the typical behaviour of a species size class. We have also provided more nuanced information, including empirical estimates of predator-prey mass ratios, relative contributions of different prey groups, and from multivariate analysis on the dissimilarity of species size class feeding traits (~~Table S3;~~ Fig. S54) which could help further unpick what such change means. This information is also widely applicable for quantifying and predicting the effects of different fishing and climate regimes where changes in the distribution of species and body sizes are anticipated (Kleisner et al., 2016; Lotze et al., 2019; Spence et al., 2021; Thompson et al., 2023).

Previous studies which identified feeding guilds used differing approaches, relied on a subset of the stomach contents data we use here and assessed different survey data to one-another (Garrison & Link, 2000a, 2000b; Thompson et al., 2020). It was therefore not clear which method would be optimal as an indicator across ecosystems. Moreover, differences in how feeding trait information has been quantified and reported has hampered the synthesis of stomach contents data. Here, we brought those different stomach contents data together by developing models to predict prey biomass and counts where information was missing. We were then able to compare different approaches to classifying feeding guilds across the datasets and apply the optimal approach to the same survey data.

This approach has helped achieve international consensus on how to assess feeding guilds across ecosystems within the OSPAR Area (Thompson, Lynam, et al., 2023). The work we present here represents a development of that pilot indicator, with improvements in how we estimated prey weights (i.e., improved modelling framework that made use of more stomach contents data) which affected feeding guild classifications; and the use of Kendall's τ trend analysis on the classified survey data (as opposed to Pearson's correlation coefficients) in order to detect correlations which may be non-linear. Many of the temporal patterns we present here are similar to those in the pilot indicator. The most notable differences appear for feeding guild species richness where values were relatively low (i.e., where relatively little change could have a large influence) in the central and northern North Sea.

We use a trend-based assessment rather than one based on reference limits. Setting thresholds for feeding guilds was outside the remit of this study and will require reference limits for Good Environmental Status to be established. This could be done through synthesising empirical evidence on feeding guild response to environmental change and human pressure (e.g., following Garrison & Link, 2000b; Thompson et al., 2020) with dynamical modelling capable of predicting ecosystem state under varying levels of human pressure (Link et al., 2010; Rossberg et al., 2017; Samhouri et al., 2010), for instance. Such work would benefit from data products capable of integrating information from different surveys, e.g., acoustic and various trawl gears, that catch a broad range of species and sizes including smaller pelagic species which are likely under-sampled by demersal trawls (Kotwicki et al., 2018; Nnanatu et al., 2020). Developing understanding of the drivers in spatial and temporal change in fish feeding behaviour (Table S1) could also be fruitful, potentially leading to the quantification of energy fluxes from different habitats (e.g., benthos and pelagic), regions, species, and seasons, for instance. Such work could help develop understanding of the connections between the wider suite of indicators which draw on different assemblages and often rely on data collected at different times and at different spatial scales (e.g., Preciado et al., 2023). The inventory of feeding interactions could also continue to develop, e.g., via surveys targeting areas and predators with limited information (e.g., Fig.

S6~~5~~; Table S5~~6~~), via DNA metabarcoding of stomach contents (Jakubavičiute et al., 2017), inference from similar predators (Gray et al., 2015; Hicks et al., 2019), biotracers (Pethybridge et al., 2018) and predictive modelling (Hernvann et al., 2022; Link, 2004; Petchey et al., 2008). Variability in digestion rates driven by environmental gradients such as temperature and differences in prey sizes and tissue composition could also be modelled to help improve estimates of biomass flux across the food web (Temming & Herrmann, 2003).

Using change in functionally distinct feeding guilds to assess environmental status has been widely advocated to fulfil OSPAR and the Marine Strategy Framework Directive requirements (Boschetti et al., 2021; ICES, 2018; Rombouts et al., 2013; Tam et al., 2017; Walmsley et al., 2016), but international consensus on how to do this has been lacking. We drew together data and expertise from across the North Atlantic and Arctic Oceans to help achieve this. In doing so, we have made empirical estimates of a range of key fish feeding traits that are widely applicable in marine ecosystem science, identified robust feeding guilds, and revealed how and where ecosystem structure and function was changing across the OSPAR Area. Such information will be critical to help better quantify and predict the effect of human pressures, such as fishing and climate change, on global patterns in marine ecosystem structure and functioning.

5 Conclusions

We mad~~k~~e use of multiple stomach contents databases to predict species- and size-specific feeding traits for fish across the North Atlantic and Arctic Oceans. We then developed a repeatable, data-driven workflow that categorised~~s~~ fish based on these feeding traits and showed how they can be applied to robustly define the feeding guilds required in OSPAR and the Marine Strategy Framework Directive guidance. This has provided an indicator capable of revealing change in ecosystem structure and function across the OSPAR Area based on routinely collected survey data. For instance, we revealed significant and spatially extensive temporal changes across the food web, with decreases in the biomass of smaller planktivorous fish which contrasted with increases in the biomass of larger more piscivorous fish. The information we have generated can be tailored to fulfil other specific evidence needs, such as improving the parametrisation of ecosystem models and quantifying sustainable levels of human pressure. Our study provides evidence supporting a candidate food web indicator for the OSPAR Area that can be readily extended to other areas and organisms.

6 Competing interests

The contact author has declared that none of the authors has any competing interests

7 Acknowledgements

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8 Authors’ contribution statement

MSAT, CL, IP, AB conceived the project; MSAT, IP, VB, AB, MC, PC, EE, GH-M, IJ, FM, SR, SS, US, BES, MAT and CL were involved in designing the methodology and collating the data; MSAT analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

9 Data availability

The data we make use of are largely publicly available, cited, and displayed alongside URLs, where applicable. We also provide all observed fish stomach contents data used in our modelling, predictions of fish feeding traits from our linear mixed effects models, haul-level estimates of feeding guild species richness, numbers of fish and their biomass based on scientific trawl surveys from the Northeast Atlantic and the temporal trend values useful for indicator reporting processes (https://doi.org/10.14466/CefasDataHub.149; Thompson et al., 2024).

10 References

Anderson, M. J. (2006). Distance-Based Tests for Homogeneity of Multivariate Dispersions. *Biometrics*, *62*(1), 245–253. https://doi.org/https://doi.org/10.1111/j.1541-0420.2005.00440.x

Arroyo, N. L., Preciado, I., López-López, L., Muñoz, I., & Punzón, A. (2017). Trophic mechanisms underlying bentho-demersal community recovery in the north-east Atlantic. *Journal of Applied Ecology*, *54*(6), 1957–1967. https://doi.org/10.1111/1365-2664.12879

Barnes, C., Maxwell, D., Reuman, D. C., & Jennings, S. (2010). Global patterns in predator-prey size relationships reveal size dependency of trophic transfer efficiency. *Ecology*, *91*(1), 222–232. https://doi.org/10.1890/08-2061.1

Boschetti, S., Piroddi, C., Druon, J., & Palialexis, A. (2021). *Marine Strategy Framework Directive – Review and analysis of Member States' 2018 reports – Descriptor 4: Food webs*. *KJ-NA-30652-EN-N (online),KJ-NA-30652-EN-C (print)*. https://doi.org/10.2760/32522 (online),10.2760/990099 (print)

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400.

Brose, U., Archambault, P., Barnes, A. D., Bersier, L. F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A., Flores, A. A. V., Fussmann, K., Gauzens, B., Gray, C., Häussler, J., Hirt, M. R., Jacob, U., Jochum, M., Kéfi, S., … Iles, A. C. (2019). Predator traits determine food-web architecture across ecosystems. *Nature Ecology and Evolution*, *3*(6), 919–927. https://doi.org/10.1038/s41559-019-0899-x

Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey, T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., … Cohen, J. E. (2006).

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CONSUMER–RESOURCE BODY-SIZE RELATIONSHIPS IN NATURAL FOOD WEBS. *Ecology*, *87*(10), 2411–2417. https://doi.org/https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2

Cachera, M., Ernande, B., Villanueva, M. C., & Lefebvre, S. (2017). Individual diet variation in a marine fish assemblage: Optimal Foraging Theory, Niche Variation Hypothesis and functional identity. *Journal of Sea Research*, *120*, 60–71. https://doi.org/https://doi.org/10.1016/j.seares.2016.08.004

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., MacE, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59–67. https://doi.org/10.1038/nature11148

Chamberlain, S. (2019). *worrms: World Register of Marine Species (WoRMS) Client* (R package version 0.4.0.).

Chamberlain, S., Szoecs, E., Foster, Z., Arendsee, Z., Boettiger, C., Ram, K., Bartomeus, I., Baumgartner, J., O'Donnell, J., & Oksanen, J. (2020). taxize: Taxonomic information from around the web. In *R package version 0.9.98* (Vol. 92). https://github.com/ropensci/taxize.

Daan, N. (1981). *Data base report of the stomach sampling project 1981. ICES Cooperative Research Report, Vol. 164. 150 pp*.

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

du Pontavice, H., Gascuel, D., Reygondeau, G., Maureaud, A., & Cheung, W. W. L. (2020). Climate change undermines the global functioning of marine food webs. *Global Change Biology*, *26*(3), 1306–1318. https://doi.org/10.1111/gcb.14944

Garrison, L. P., & Link, J. S. (2000a). Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Marine Ecology Progress Series*, *202*, 231–240. https://doi.org/10.3354/meps202231

Garrison, L. P., & Link, J. S. (2000b). Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region. *ICES Journal of Marine Science*, *57*(3), 723–730. https://doi.org/10.1006/jmsc.2000.0713

Gray, C., Figueroa, D. H., Hudson, L. N., Ma, A., Perkins, D., & Woodward, G. (2015). Joining the dots: An automated method for constructing food webs from compendia of published interactions. *Food Webs*, *5*, 11–20. https://doi.org/10.1016/j.fooweb.2015.09.001

Hartig, F. (2022). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Hernvann, P.-Y., Gascuel, D., Kopp, D., Robert, M., & Rivot, E. (2022). EcoDiet: A hierarchical Bayesian model to combine stomach, biotracer, and literature data into diet matrix estimation. *Ecological Applications*, *32*(2), e2521. https://doi.org/https://doi.org/10.1002/eap.2521

Hicks, C. C., Cohen, P. J., Graham, N. A. J., Nash, K. L., Allison, E. H., D'Lima, C., Mills, D. J., Roscher, M., Thilsted, S. H., Thorne-Lyman, A. L., & MacNeil, M. A. (2019). Harnessing global fisheries to tackle micronutrient deficiencies. *Nature*, *574*(7776), 95–98. https://doi.org/10.1038/s41586-019-1592-6

Hijmans, R. J., Williams, E., & Vennes, C. (2021). *geosphere: spherical trigonometry. R package geosphere version 1.5-10. 2019*.

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R. M., Schuetzenmeister, A., Scheibe, S., & Hothorn, M. T. (2016). Package 'multcomp.' In *Simultaneous inference in general parametric models. Project for Statistical Computing, Vienna, Austria*.

ICES. (1997). *Database report of the stomach sampling project, 1991. ICES Cooperative Research Report, Vol. 219. 426 pp*. https://doi.org/https://doi.org/10.17895/ices.pub.4626

ICES. (2018). *Report of the Working Group on Ecosystem Effects of Fishing Activities (WGECO)*. 12–19 April 2018, San Pedro del Pinatar, Spain. ICES CM 2018/ACOM:27. 69 pp.

Jakubavičiute, E., Bergström, U., Eklöf, J. S., Haenel, Q., & Bourlat, S. J. (2017). DNA metabarcoding reveals diverse diet of the three-spined stickleback in a coastal ecosystem. *PLoS ONE*, *12*(10), e0186929. https://doi.org/10.1371/journal.pone.0186929

Katara, I., Peden, W. J., Bannister, H., Ribeiro, J., Fronkova, L., Scougal, C., Martinez, R., Downie, A. L., & Sweeting, C. J. (2021). Conservation hotspots for fish habitats: A case study from English and Welsh waters. *Regional Studies in Marine Science*, *44*, 101745. https://doi.org/10.1016/j.rsma.2021.101745

Kleisner, K. M., Fogarty, M. J., McGee, S., Barnett, A., Fratantoni, P., Greene, J., Hare, J. A., Lucey, S. M., McGuire, C., Odell, J., Saba, V. S., Smith, L., Weaver, K. J., & Pinsky, M. L. (2016). The Effects of Sub-Regional Climate Velocity on the Distribution and Spatial Extent of Marine Species Assemblages. *PLOS ONE*, *11*(2), e0149220-. https://doi.org/10.1371/journal.pone.0149220

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1814). https://doi.org/10.1098/rspb.2015.1546

Kotwicki, S., Ressler, P. H., Ianelli, J. N., Punt, A. E., & Horne, J. K. (2018). Combining data from bottom-trawl and acoustic-trawl surveys to estimate an index of abundance for semipelagic species. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(1), 60–71. https://doi.org/10.1139/cjfas-2016-0362

Legendre, P. (1998). Model II regression user's guide, R edition. *R Vignette*, *14*. https://cran.r-project.org/web/packages/lmodel2/vignettes/mod2user.pdf

Link, J. S. (2004). A General Model of Selectivity for Fish Feeding: A Rank Proportion Algorithm. *Transactions of the American Fisheries Society*, *133*(3), 655–673. https://doi.org/10.1577/t02-142.1

Link, J. S., Fulton, E. A., & Gamble, R. J. (2010). The northeast US application of ATLANTIS: A full system model exploring marine ecosystem dynamics in a living marine resource management context. *Progress in Oceanography*, *87*(1), 214–234. https://doi.org/https://doi.org/10.1016/j.pocean.2010.09.020

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Galbraith, E. D., Barange, M., Barrier, N., Bianchi, D., Blanchard, J. L., Bopp, L., Büchner, M., Bulman, C. M., Carozza, D. A., Christensen, V., Coll, M., Dunne, J. P., Fulton, E. A., Jennings, S., … Worm, B. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences*, *116*(26), 12907–12912. https://doi.org/10.1073/pnas.1900194116

Lynam, C. P., & Piet, G. (2022). Pilot Assessment of Mean Maximum Length of Fish. In *OSPAR, 2023: The 2023 Quality Status Report for the North-East Atlantic*. OSPAR Commission, London. https://doi.org/https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/mean-max-fish-pilot/

Lynam, C. P., Piet, G., & Volwater, J. (2022). Size Composition in Fish Communities. In *OSPAR, 2023: The 2023 Quality Status Report for the Northeast Atlantic*. OSPAR Commission, London. https://doi.org/https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/size-composition-fish-communities

Lynam, C. P., & Ribeiro, J. (2022). *A data product derived from Northeast Atlantic groundfish data from scientific trawl surveys 1983-2020*. https://doi.org/https://doi.org/10.14466/CefasDataHub.126

Nakazawa, T., Ushio, M., & Kondoh, M. (2011). Scale Dependence of Predator-Prey Mass Ratio. Determinants and Applications. In *Advances in Ecological Research* (1st ed., Vol. 45). Elsevier Ltd. https://doi.org/10.1016/B978-0-12-386475-8.00007-1

Nnanatu, C. C., Thompson, M. S. A., Spence, M. A., Couce, E., van der Kooij, J., & Lynam, C. P. (2020). Bayesian hierarchical space-time models to improve multispecies assessment by combining observations from disparate fish surveys. *ArXiv*. http://arxiv.org/abs/2012.02196

Otto, S. B., Rall, B. C., & Brose, U. (2007). Allometric degree distributions facilitate food-web stability. *Nature*, *450*(7173), 1226–1229. https://doi.org/10.1038/nature06359

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Pecuchet, L., Blanchet, M. A., Frainer, A., Husson, B., Jørgensen, L. L., Kortsch, S., & Primicerio, R. (2020). Novel feeding interactions amplify the impact of species redistribution on an Arctic food web. *Global Change Biology*, *26*(9), 4894–4906. https://doi.org/10.1111/gcb.15196

Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.0710672105

Pethybridge, H. R., Choy, C. A., Polovina, J. J., & Fulton, E. A. (2018). Improving Marine Ecosystem Models with Biochemical Tracers. *Annual Review of Marine Science*, *10*(1), 199–228. https://doi.org/10.1146/annurev-marine-121916-063256

Pinnegar, J. K. (2019). *DAPSTOM - An Integrated Database & Portal for Fish Stomach Records. Version 5.5*.

Pomeranz, J. P. F., Thompson, R. M., Poisot, T., & Harding, J. S. (2019a). Inferring predator–prey interactions in food webs. *Methods in Ecology and Evolution*, *10*(3), 356–367. https://doi.org/10.1111/2041-210X.13125

Pomeranz, J. P. F., Thompson, R. M., Poisot, T., & Harding, J. S. (2019b). Inferring predator–prey interactions in food webs. *Methods in Ecology and Evolution*, *10*(3), 356–367. https://doi.org/10.1111/2041-210X.13125

Preciado, I., López-López, L., Rabanal, I., Ortiz, J. J., Torres, M. Á., Muñoz, I., Iglesias, D., García Rebollo, J. M., Mendes, H., Le Loc'h, F., Garrido, S., Metaireau, H., & Serre, S. (2023). Changes in average trophic level of marine consumers. In *OSPAR, 2023: The 2023 Quality Status Report for the North-East Atlantic*. OSPAR Commission.

R Core Team. (2020). *R: A language and environment for statistical computing. R Foundation for Statistical Computing*.

Reum, J. C. P., Holsman, K. K., Aydin, K. Y., Blanchard, J. L., & Jennings, S. (2019). Energetically relevant predator–prey body mass ratios and their relationship with predator body size. *Ecology and Evolution*, *9*(1), 201–211. https://doi.org/10.1002/ece3.4715

Rombouts, I., Beaugrand, G., Fizzala, X., Gaill, F., Greenstreet, S. P. R., Lamare, S., Le Loc'H, F., McQuatters-Gollop, A., Mialet, B., Niquil, N., Percelay, J., Renaud, F., Rossberg, A. G., & Féral, J. P. (2013). Food web indicators under the Marine Strategy Framework Directive: From complexity to simplicity? *Ecological Indicators*, *29*, 246–254. https://doi.org/10.1016/j.ecolind.2012.12.021

Rooney, N., McCann, K., Gellner, G., & Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature*, *442*(7100), 265–269. https://doi.org/10.1038/nature04887

Rossberg, A. G., Uusitalo, L., Berg, T., Zaiko, A., Chenuil, A., Uyarra, M. C., Borja, A., & Lynam, C. P. (2017). Quantitative criteria for choosing targets and indicators for sustainable use of ecosystems. *Ecological Indicators*, *72*, 215–224. https://doi.org/https://doi.org/10.1016/j.ecolind.2016.08.005

Samhouri, J. F., Levin, P. S., & Ainsworth, C. H. (2010). Identifying Thresholds for Ecosystem-Based Management. *PLOS ONE*, *5*(1), e8907-. https://doi.org/10.1371/journal.pone.0008907

Schneider, F. D., Scheu, S., & Brose, U. (2012). Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters*, *15*(5), 436–443. https://doi.org/10.1111/j.1461-0248.2012.01750.x

Scott, F., Blanchard, J. L., & Andersen, K. H. (2014). mizer: an R package for multispecies, trait-based and community size spectrum ecological modelling. *Methods in Ecology and Evolution*, *5*(10), 1121–1125. https://doi.org/https://doi.org/10.1111/2041-210X.12256

Smith, B. E., & Link, J. S. J. (2010). The Trophic Dynamics of 50 Finfish and 2 Squid Species on the Northeast US Continental Shelf. *U.S. Dep. Commer. NOAA Technical Memorandum*, *NMFS-NE-21*(May), 1–29.

Spence, M. A., Griffiths, C. A., Waggitt, J. J., Bannister, H. J., Thorpe, R. B., Rossberg, A. G., & Lynam, C. P. (2021). Sustainable fishing can lead to improvements in marine ecosystem status: an ensemble-model forecast of the North Sea ecosystem. *Marine Ecology Progress Series*, *680*, 207–221. https://www.int-res.com/abstracts/meps/v680/p207-221/

Tam, J. C., Link, J. S., Rossberg, A. G., Rogers, S. I., Levin, P. S., Rochet, M. J., Bundy, A., Belgrano, A., Libralato, S., Tomczak, M., Van De Wolfshaar, K., Pranovi, F., Gorokhova, E., Large, S. I., Niquil, N., Greenstreet, S. P. R., Druon, J. N., Lesutiene, J., Johansen, M., … Rindorf, A. (2017). Towards ecosystem-based management: Identifying operational food-web indicators for marine ecosystems. *ICES Journal of Marine Science*, *74*(7), 2040–2052. https://doi.org/10.1093/icesjms/fsw230

Temming, A., & Herrmann, J. P. (2003). Gastric evacuation in cod. Prey-specific evacuation rates for use in North Sea, Baltic Sea and Barents Sea multi-species models. *Fisheries Research*, *63*(1), 21–41. https://doi.org/10.1016/s0165-7836(03)00041-9

Thompson, M. S. A., Couce, E., Schratzberger, M., & Lynam, C. P. (2023). Climate change affects the distribution of diversity across marine food webs. *Global Change Biology*, *29*(23), 6606–6619. https://doi.org/https://doi.org/10.1111/gcb.16881

Thompson, M. S. A., Lynam, C. P., & Preciado, I. (2023). *Pilot Assessment of Feeding Guilds. In: OSPAR, 2023: The 2023 Quality Status Report for the Northeast Atlantic*. https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/feeding-guild-pilot-assessment

Thompson, M. S. A., Pontalier, H., Spence, M. A., Pinnegar, J. K., Greenstreet, S. P. R., Moriarty, M., Hélaouët, P., & Lynam, C. P. (2020). A feeding guild indicator to assess environmental change impacts on marine ecosystem structure and functioning. *Journal of Applied Ecology*, *57*(9), 1769–1781. https://doi.org/10.1111/1365-2664.13662

Thompson, M. S. A., Preciado, I., Maioli, F., Bartolino, V., Belgrano, A., Casini, M., Cresson, P., Eriksen, E., Hernandez-Milian, G., Jónsdóttir, I. G., Neuenfeldt, S., Pinnegar, J. K., Ragnarsson, S., Schückel, S., Schückel, U., Smith, B. E., Torres, M. Á., Webb, T. J., & Lynam, C. P. (2024). *Modelled and observed fish feeding traits for the North Atlantic and Arctic Oceans (1836-2020) and population estimates of fish with different feeding traits from Northeast Atlantic scientific trawl surveys (1997-2020)*. Cefas, UK. V1. doi: https://doi.org/10.14466/CefasDataHub.149

Timmerman, C.-A., Marchal, P., Denamiel, M., Couvreur, C., & Cresson, P. (2020). Seasonal and ontogenetic variation of whiting diet in the Eastern English Channel and the Southern North Sea. *PLOS ONE*, *15*(9), e0239436-. https://doi.org/10.1371/journal.pone.0239436

Torres, M. Á., Coll, M., Heymans, J. J., Christensen, V., & Sobrino, I. (2013). Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (South-western Spain). *Ecological Modelling*, *265*, 26–44. https://doi.org/10.1016/j.ecolmodel.2013.05.019

Travers-Trolet, M. (2017). *CGFS2017 cruise, RV Thalassa*.

Verin, Y. (2018). *IBTS 2018 cruise, RV Thalassa*.

Walmsley, S., Weiss, A., Claussen, U., & Connor, D. (2016). Guidance for Assessments Under Article 8 of the Marine Strategy Framework Directive. *Integration of Assessment Results. A Report Produced for the European Commission, DG Environment.*

Wang, S., & Brose, U. (2018). Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. *Ecology Letters*, *21*(1), 9–20. https://doi.org/10.1111/ele.12865

Webb, T. J., & Vanhoorne, B. (2020). Linking dimensions of data on global marine animal diversity: Dimensions of global marine diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1814), 20190445. https://doi.org/10.1098/rstb.2019.0445rstb20190445

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology and Evolution*, *20*(7), 402–409. https://doi.org/10.1016/j.tree.2005.04.005

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J., & Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science*, *314*(5800), 787–790. https://doi.org/10.1126/science.1132294

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