1 # Fish functional groups of the North Atlantic and Arctic Oceans

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35

36   **Abstract**

37   International efforts to assess the status of marine ecosystems have been hampered by insufficient

38   observations of food web interactions across many species, their various life stages, and geographic

39   ranges. Hence, we collated data from multiple databases of fish stomach contents from samples taken

40   across the North Atlantic and Arctic Oceans containing 944,129 stomach samples from larvae to

41   adults, with 14,196 unique interactions between 227 predator species and 2158 prey taxa. We use

42   these data to develop a data-driven, reproducible approach to classifying broad functional feeding

43   guilds and then apply these to fish survey data from the Northeast Atlantic shelf seas to reveal spatial

44   and temporal changes in ecosystem structure and functioning. In doing so, we construct predator-

45   prey body size scaling models to predict the biomass of prey functional groups, e.g., zooplankton,

46   benthos, and fish, for different predator species. These predictions provide empirical estimates of

47   species- and size-specific feeding traits of fish, such as predator-prey mass ratios, individual prey mass,

48   and the biomass contribution of different prey to predator diets. The functional groupings and feeding

49   traits provided here help to further resolve our understanding of interactions within marine food webs

50   and support the use of trait-based indicators in biodiversity assessments. The data used and

51   predictions generated in this study are published on the Cefas Data Hub at:

52   https://doi.org/10.14466/CefasDataHub.149 (Thompson et al., 2024).

53

54 Keywords: feeding guilds; species traits; marine ecosystem structure and functioning; food web

55 indicator; biodiversity; trophic interactions; stomach contents data.

56

1 Introduction

57
58
59 Human pressures are affecting global patterns in marine ecosystem structure and functioning, from

60 species distributions and their body sizes, to how and where energy fluxes through food webs

61 (Daufresne et al., 2009; du Pontavice et al., 2020; Kortsch et al., 2015). Grouping organisms into broad

62 functional feeding guilds and assessing change in their populations has been widely advocated to

63 assess marine ecosystem status, gauge sustainable levels of human pressure, and inform management

64 interventions (ICES, 2018; Rombouts et al., 2013; Tam et al., 2017). Yet, international efforts to

65 develop indicators of marine ecosystem status have been hampered by the large number of

66 observations needed to understand food web processes involving many species, their various life

67 stages, and geographic ranges.

68 Despite the complexity of natural food webs, their structure and dynamics are largely determined by

69 the size of the interacting organisms because predators are systematically larger than their prey,

70 especially in aquatic ecosystems (Brose et al., 2006; Petchey et al., 2008; Woodward et al., 2005). The

71 behaviour of organisms relating to their evolutionary history, including adaptations for specific

72 foraging strategies and habitats, also affects predator-prey interactions (Brose et al., 2019; Link, 2004;

73 Pecuchet et al., 2020; Pomeranz et al., 2019). Fish fulfil many different roles in an ecosystem (Katara

74 et al., 2021), often starting life as planktivores which feed lower in the food web, with some species

75 developing into intermediate (e.g., benthivores) and higher predator feeding guilds (e.g., piscivores)

76 which consume larger prey as they grow. Fish feeding guild biomasses are also responsive to human

77 pressures including fishing and climate change (Garrison & Link, 2000a, 2000b; Thompson et al., 2020).

78 Analysing change in fish feeding guild biomass can, therefore, provide simultaneous information on

79 ecosystem structure and functioning, by revealing temporal change in the spatial distribution of, e.g.,

80   planktivore biomass (structure) which is also indicative of change in energy flux between plankton and

81   fish (functioning). Change in feeding guild species richness provides a measure of functional

82   redundancy where, for instance, relatively low and decreasing values highlight areas where a function

83   is supported by only a few species and is at risk.

84   Internationally coordinated surveys with observations on fish species distributions, body sizes and

85   biomass provide extensive data to assess change in fish feeding guilds (Lynam & Ribeiro, 2022).

86   Complementing these, many fish stomach content data that contain information on food web

87   interactions have been collected across the North Atlantic and Arctic Oceans (Arroyo et al., 2017;

88   Cachera et al., 2017; ICES, 1997; Pinnegar, 2019; Smith & Link, 2010; Torres et al., 2013). However,

89   idiosyncrasies in how feeding information has been quantified and reported across different stomach

90   content databases have hampered efforts to depict general feeding traits. Specifically, four feeding

91   guilds relevant to fish are used in OSPAR (The Convention for the Protection of the Marine

92   Environment of the North-East Atlantic) and EU's MSFD (Marine Strategy Framework Directive)

93   reporting processes, but without an agreed, data-driven method to categorise predators into them

94   (i.e., planktivores, sub-apex demersal, sub-apex pelagic and apex predators; Boschetti et al., 2021;

95   Walmsley et al., 2016; see also https://oap.ospar.org/en/resource-catalogue/enumeration-

96   tables/cemp-enumeration-tables/). Any macroecological assessment of feeding guilds may therefore

97   be confounded because changes could have a methodological basis. This has constrained the

98   contribution of food web indicators to marine ecosystem status assessment.

99   The body size scaling relationship between predators and their prey offers a means to depict general

100 feeding traits across many species, their various life stages, and geographic ranges that have so far

101 been lacking. Predator-prey body size scaling is also important to measure empirically because it can

102 affect the pathway and quantity of energy flux through a food web (Barnes et al., 2010; Brose et al.,

103 2019; Nakazawa et al., 2011; Schneider et al., 2012). Predators feeding on relatively small prey with

104 high predator-prey mass ratios (PPMR) can dampen strong oscillatory dynamics and thus help to

105 maintain stability in food webs (Otto et al., 2007; Rooney et al., 2006) and ecosystem functioning

106 (Nakazawa et al., 2011; Schneider et al., 2012; Wang & Brose, 2018). Moreover, both predator and

107 prey taxonomy and their traits can be used to predict interactions with typically high PPMRs that may

108 be particularly important (Brose et al., 2019; Reum et al., 2019). For instance, we anticipate that

109 planktivorous and benthivorous fish will have some of the highest PPMRs, especially those that remain

110 in the same feeding guild through ontogeny, while fish species which develop into piscivores could

111 see the largest change (a decrease) in their PPMR across their body size range.

112 Here we make use of predator-prey body size scaling relationships to draw on multiple stomach

113 content databases and derive comparable fish feeding trait information for the North Atlantic and

114 Arctic Oceans. This new data collation contains observations from 944,129 fish stomachs collected

115 between 1836 - 2020. We use these feeding traits to categorise fish into feeding guilds in a way that

116 is conducive to their application internationally, across ecosystems. Feeding guilds are then applied to

117 survey data collected from across the northeast Atlantic shelf seas to demonstrate macroecological

118 patterns in ecosystem structure and functioning relevant to status assessment advocated by OSPAR.

119 We test the following hypotheses: i) intra and interspecific body size scaling for predator species is

120 dependent on prey group (e.g., plankton, benthos, and fish prey); ii) multiple distinct feeding guilds

121 are evident based on feeding trait data; iii) feeding guilds capture significant spatio-temporal trends

122 in survey data. Our aim was twofold: to generate empirical estimates of fish feeding traits that could

123 help improve understanding of changes in marine ecosystem structure and functioning; and to achieve

124 international consensus on the best approach to assessing feeding guilds across ecosystems within

125 the OSPAR Maritime Area and in a way that can be readily extended to other areas (e.g., Northeast

126 US continental shelf) and organisms (e.g., invertebrates and mammals).

127

128 ## 2 Methods
129
130 ### 2.1 Stomach contents data
131
132 We draw together stomach contents data primarily collected from the North Atlantic shelf seas, with

133 important contributions from the Baltic, Barents and Norwegian Seas (Fig. 1, S1). These data were

134   sourced from a combination of previously published and unpublished data including DAPSTOM

135   (Pinnegar, 2019), ICES Year of the Stomach (Daan, 1981; ICES, 1997), the Northeast US continental

136   shelf (Smith & Link, 2010), Northern Spanish shelf (Arroyo et al., 2017), Gulf of Cadiz (Torres et al.,

137   2013), Swedish-, Icelandic-, Norwegian-, French- (Cachera et al., 2017; Timmerman et al., 2020;

138   Travers-Trolet, 2017; Verin, 2018) and German-led surveys (e.g., FishNet, https://www.nationalpark-

139   wattenmeer.de/wissensbeitrag/fishnet/). We have included stomach contents data from outside the

140   OSPAR Area (i.e., Northeast US continental shelf and Baltic Sea) to demonstrate the wider applicability

141   of our approach to defining feeding guilds and because those data have been used to classify feeding

142   guilds previously (Garrison & Link, 2000a). The full data collation contains observations from larvae

143   (<1 g) to adults (up to 351 kg), representing 14,196 unique interactions between 227 predator species

144   and 2158 prey taxa (https://doi.org/10.14466/CefasDataHub.149; Thompson et al., 2024). We provide

145   a summary of data sources, spatial and temporal ranges, and sample distributions in Table 1. All data

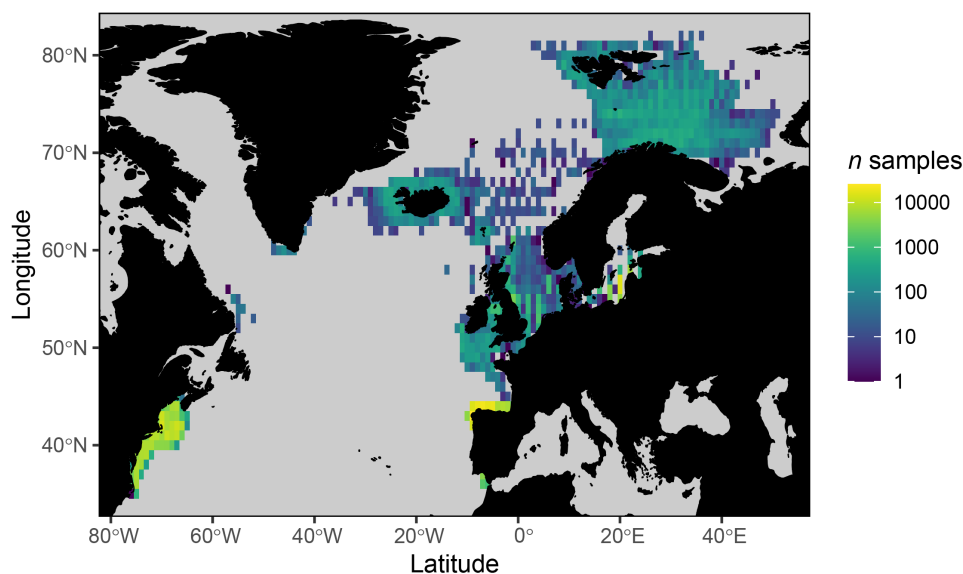
146   processing and subsequent analyses were conducted in R version 4.02 (R Core Team, 2020). Predator

147   and prey taxonomy were processed using the "taxize" package (Chamberlain et al., 2020) and assigned

148   to 'zooplankton', 'benthos', 'fish', 'nekton' and 'other' functional groups after Webb & Vanhoorne

149   (2020) using the "worrms" package (Chamberlain, 2019).

150

151

152
153 Figure 1: Number of stomach samples on a 1° longitudinal by 1° latitudinal grid.

154
155 Table 1. A summary of data sources, spatial and temporal ranges, and sample distributions (see also
156 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

157

158 2.2 Quantifying intra- and interspecific body size scaling relationships between predators and
159 different prey functional groups

160
161 Prey count and biomass observations (wet weight in grams) are needed to estimate predator-prey

162 mass ratios (PPMR), but these were available for only 56% of the stomach contents data. Therefore,

163 to make use of all the data (Fig. 1; Table 1) when assigning fish to feeding guilds, a linear mixed effect

164 model of predator-prey body size scaling was constructed to estimate prey counts or biomass where

165 either were unavailable; using only data where taxonomy for both predator and prey was resolved

166 (i.e., to species and functional group, respectively), and predator body size, prey body size and prey

167 counts were all available. Major axis regression following Brose *et al.* (2019) was not suitable because

168 we needed to make predictions of prey body size and minimise the squared residuals in the response

169 (Legendre, 1998). Log_{10} transformed individual prey mass (wet weight in g) was fit as the response,

170 with an interaction term between log_{10} transformed predator body mass (wet weight in g). Random

171 intercepts and slopes were fit for both predator taxa or prey functional group to test if either

172 interacted with predator body mass. Random intercepts were fit for datasets to test for systematic

173 differences in how data were generated: grouped into those from Spain, USA, and ICES, which each

174 follow their own protocols for measuring prey biomass, and all others which represent a mixture of

175 methods from across studies. Random intercepts were also fit for years, sites (a 3 by 3 grid across the

176 study area based on splitting the gradients of longitude and latitude into 3 equal lengths; Fig S1) and

177 the number of stomachs sampled with two levels, 1 = from multiple stomachs and 2 = were stomach

178 samples were pooled (some stomach samples contained in DAPSTOM and ICES Year of the Stomach

179 were pooled at the point of collection for size classes of predator species). We use a Student's t-

180 distribution to account for heavy tails in the distribution of the response. The Akaike Information

181 Criterion (AIC) was used on nested models to assess the importance of all predictors. The full model

182 had the lowest AIC by >2 units meaning all predictors were retained (Table S1). Model diagnostic plots

183 were performed using the R package *DHARMa* (Hartig, 2022).

184 The 'full' model was used to predict the mean individual body mass of prey functional groups for

185 predator species of a given size. This enabled us to make use of many observations in DAPSTOM, for

186 instance, which have recorded prey counts but no prey biomass. In such cases, we estimated the

187 biomass of each prey taxa by multiplying the predicted mean individual body mass for their functional

188 group by the observed prey count. Where prey counts were missing, e.g., much of the data from Smith

189 & Link (2010; USA data in Fig. S1), we estimate these by dividing the observed biomass of each prey

190 taxa by the predicted mean individual prey mass for their functional group. We provide R script and

191   the data underlying our model, with an example showing how to predict individual prey size based on

192   a   list   of   predator   taxa,   predator   sizes   and   prey   functional   groups

193   (https://github.com/MurraySAThompson/fish-feeding-traits-glmm). Our full model has temporal and

194   spatial information as random effects because we were interested in developing general feeding traits

195   for the study area, irrespective of spatial and temporal gradients. However, the significance of spatial

196   and temporal random effects (Table S1) suggests future work exploring environmental change drivers

197   of predator-prey scaling could be fruitful. All linear mixed effects models were fit using the *glmmTMB*

198   R package (Brooks et al., 2017).

199

200   2.3 Classifying predator feeding guilds based on feeding trait data
201
202   Predators were categorised by species and size. We use 20 equal size bins to categorise predator mass

203   along a $\log_{10}$ transformed gradient from 0.1 micrograms to 190 tonnes, capable of capturing organisms

204   from plankton to blue whales (Table S2). Data for each species size class was then estimated across all

205   available stomach samples (Fig. 1; Table 1), with means calculated for % prey functional group

206   biomass, biomass weighted PPMR (after Reum et al., 2019) and mean individual prey mass (Table S3).

207   We used directly observed data where available and predictions from our predator-prey body size

208   scaling models where data were missing. Feeding guilds were assigned based on cluster analysis using

209   the 'ward D2' agglomeration method on Bray-Curtis dissimilarities between predator diets available

210   in the R *stats* package (R Core Team, 2020).

211   We compared different methods to classifying feeding guilds where the dissimilarity matrix used in

212   the cluster analysis was generated using either: 1) the biomass of prey taxa (Garrison & Link, 2000a);

213   2) prey taxa occurrence (Thompson et al., 2020) or; 3) via a novel method where dissimilarities are

214   based on broad feeding traits (henceforth, the biomass, occurrence and trait methods). Feeding traits

215   were $\log_{10}$ transformed mean individual prey mass (g), $\log_{10}$ transformed mean biomass weighted

216   PPMR, and the mean % biomass contribution to the stomach contents of zooplankton (including fish

217   <0.5g), benthos, nekton (other than fish) and fish (all fish prey ≥ 0.5g); with all variables rescaled to

218   values of or between 0 and 1. We tested for differences between these methods to classifying feeding

219   guilds by comparing them after re-sampling (n = 1000) subsets of the data (n = 30 unique stomach

220   samples per predator). Predators with fewer than 30 samples were not classified into feeding guilds.

221   Compositional change in predators between successively reclassified feeding guilds was used to

222   determine the ability of each method to consistently classify similar predators in the same guild.

223   Compositional change was measured using the distance to centroid following analysis of multivariate

224   homogeneity of groups dispersions (Anderson, 2006). The method with the lowest mean distance to

225   centroid was determined to have the most robust feeding guild classifications as determined using

226   analysis of variance tests. First, we tested whether compositional change across feeding guilds was

227   non-random for each method: distance to centroid (i.e., compositional change) was the response,

228   with 'Guild', and 'Data' (i.e., a factor identifying each unique re-sampling event) as predictors. We then

229   tested for significant differences between methods: distance to centroid (i.e., compositional change)

230   was the response, with 'Method', 'Guild', and 'Data' as predictors. Significant predictors were

231   determined using the F-test on nested models. Targeted tests for differences between the mean

232   distance to centroid across methods were carried out using Tukey's all-pairwise comparisons that

233   corrects for multiple comparisons in the "multcomp" package (Hothorn et al., 2016).

234   The ability to classify common feeding guilds across ecosystems (e.g., sub-apex and apex predators)

235   rather than area-specific guilds (e.g., a feeding guild unique to the North Sea) is another important

236   quality for a feeding guild indicator to exhibit. We assessed how important spatial gradients were in

237   our three different approaches to classifying feeding guilds. First, we generated latitudinal and

238   longitudinal coordinate centroids for each predator by taking a mean across their stomach samples.

239   We then took a mean across these predator centroids to generate a centroid for all the data, and also

240   means across these predator centroids but grouped by feeding guild and method to generate method-

241   specific guild centroids. Next, we measured the distance between the overall data centroid to the

242   method-specific guild centroids using the *geosphere* package (Hijmans et al., 2021) and summed

243   distances for each method. A large sum of distances for a method to the overall data centroid would

244   indicate that feeding guilds were area-specific, largely made up of predators found close together, and

245   thus spatial gradients would be important determinants of feeding guild structure. The method with

246   the lowest sum of distances to the overall data centroid was deemed to be least affected by spatial

247   gradients and thus preferred.

248   Four feeding guilds have been called for in OSPAR and MSFD guidance, i.e., planktivores, sub-apex

249   demersal, sub-apex pelagic and apex predators (Boschetti et al., 2021; Walmsley et al., 2016; see also

250   https://oap.ospar.org/en/resource-catalogue/enumeration-tables/cemp-enumeration-tables/),

251   without consensus on how to categorise predators into these guilds. We use four feeding guilds here

252   to help bridge this gap and so that we can elegantly capture a broad set of ecosystem components

253   while exploring guild responses in biomass and species richness in the survey data. Changing the

254   number of feeding guilds could be justified, depending on the question, and is straightforward to

255   implement by taking a higher or lower split in the classification tree. We see this as a strength of our

256   approach because feeding guilds are hierarchically structured much like how taxonomic or other trait

257   information has been organised. We provide a table which details the branches for up to five feeding

258   guilds so future assessments can choose which level of complexity suits their need. We also present

259   axis scores from a non-metric multidimensional scaling analysis of the dissimilarities used in our

260   cluster analysis which provide a more nuanced understanding (i.e., bounded data as opposed to

261   categorical) of different predator feeding traits in relation to others. Moreover, because it is a data-

262   driven, reproducible approach, new information can be systematically integrated to 1) further resolve

263   differences in feeding traits, 2) feeding guild composition and 3) test if changes in predator feeding

264   traits provides evidence for spatially or temporally flexible classifications.

265

266   2.4 Using feeding guilds to capture spatiotemporal trends in survey data
267

268   The new feeding guild classifications have been applied to processed otter trawl survey data for the

269   Northeast Atlantic shelf seas collected between 1997–2020 (Lynam & Ribeiro, 2022) to reveal spatial

270   and temporal patterns in feeding guild responses. These survey data have been processed specifically

271   to support state indicators, with observations for the biomass of species size classes standardised to

272   the area swept for each haul. Survey data corresponding with all our stomach content data, from north

273   of Norway, Icelandic waters, the Baltic Sea and eastern shelf seas of the USA, have not yet been

274   standardised and processed in the same way, hence why we haven't included them here. Extending

275   this work to assess change in ecosystem structure and function across the study region covered by the

276   stomach contents data (Fig. 1) represents a key area for future development.

277   Compared with quarter 2 and 3 (April – September), data from quarters 1 and 4 (January-March and

278   October – December, respectively) typically have longer time-series available over much of the study

279   region and so were preferentially selected. Where data from quarters 1 or 4 were not available, otter

280   trawl data from other quarters were used. Table S4 provides information on the surveys used and

281   their spatial and temporal ranges. The temporal assessment covers 1997-2020 because the majority

282   of the surveys considered have at least a near complete time-series covering that period. Longer time-

283   series do exist for some surveys but including these data would mean we are looking at long-term

284   change for some areas, but shorter-term change for others which could confound interpretation.

285   Spatial and temporal change in feeding guild responses were determined for the Greater North Sea,

286   Celtic Seas, Bay of Biscay and Iberian Coast, and the wider Atlantic. The assessment strata used here

287   replicate those used for the OSPAR food web indicators: mean-maximum length and size-composition

288   in fish communities (Lynam et al., 2022; Lynam & Piet, 2022).

289   Kendall's τ trend analysis was used to identify areas of significant temporal change in feeding guild

290   responses based on the relationship between mean haul-level values of feeding biomass and species

291   richness for each assessment strata and year. Kendall's τ scores of −1 to +1 represent a 100%

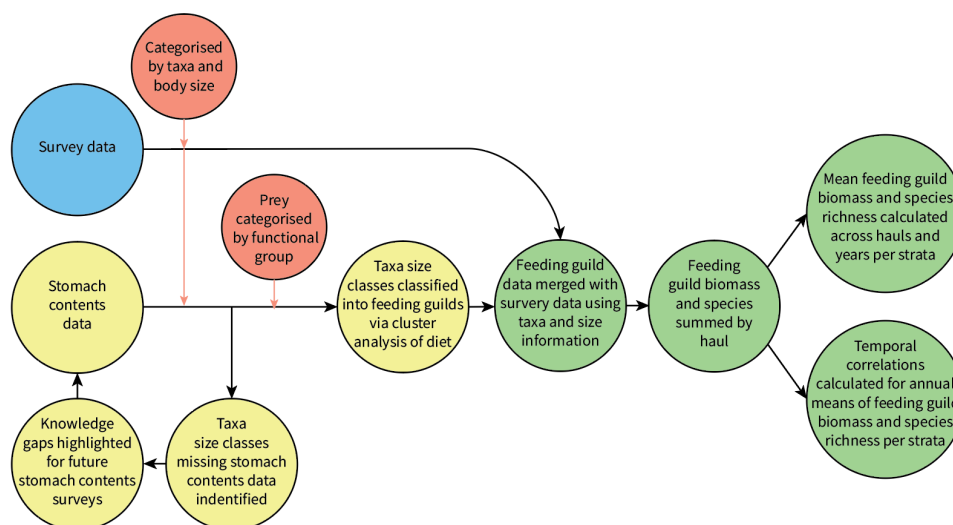
292   probability of a decreasing or increasing trend, respectively. By using Kendall's τ, which is rank-based

293   and non-parametric, we can detect correlations which may be non-linear. Stomach contents data,

294   prey size predictions, haul-level estimates of feeding guild biomass and their species richness along

295   with   Kendall's   τ   correlation   coefficients   and   *p*   have   all   been   made   available

296   (https://doi.org/10.14466/CefasDataHub.149; Thompson et al., 2024).

297

298
299 Figure 2: The process used to classify feeding guilds based on predator stomach contents data, assign
300 them to survey data and calculate feeding guild responses across the assessment strata. Yellow circles
301 = stomach contents data, blue circle = otter trawl survey data, green circles = survey data with feeding
302 guild information appended.
303

304 ## 3 Results
305
306 3.1 Unique intra- and interspecific body size scaling relationships between predators and prey
307 functional groups
308
309 There were significant differences in the $\log_{10}$ transformed scaling relationship between predator and

310 prey body mass captured by the interactions between predator body mass and predator species and

311 prey functional group combinations (Fig. 3). These results support our first hypothesis that predator

312 species can have unique intra- and interspecific body size scaling relationships with different prey

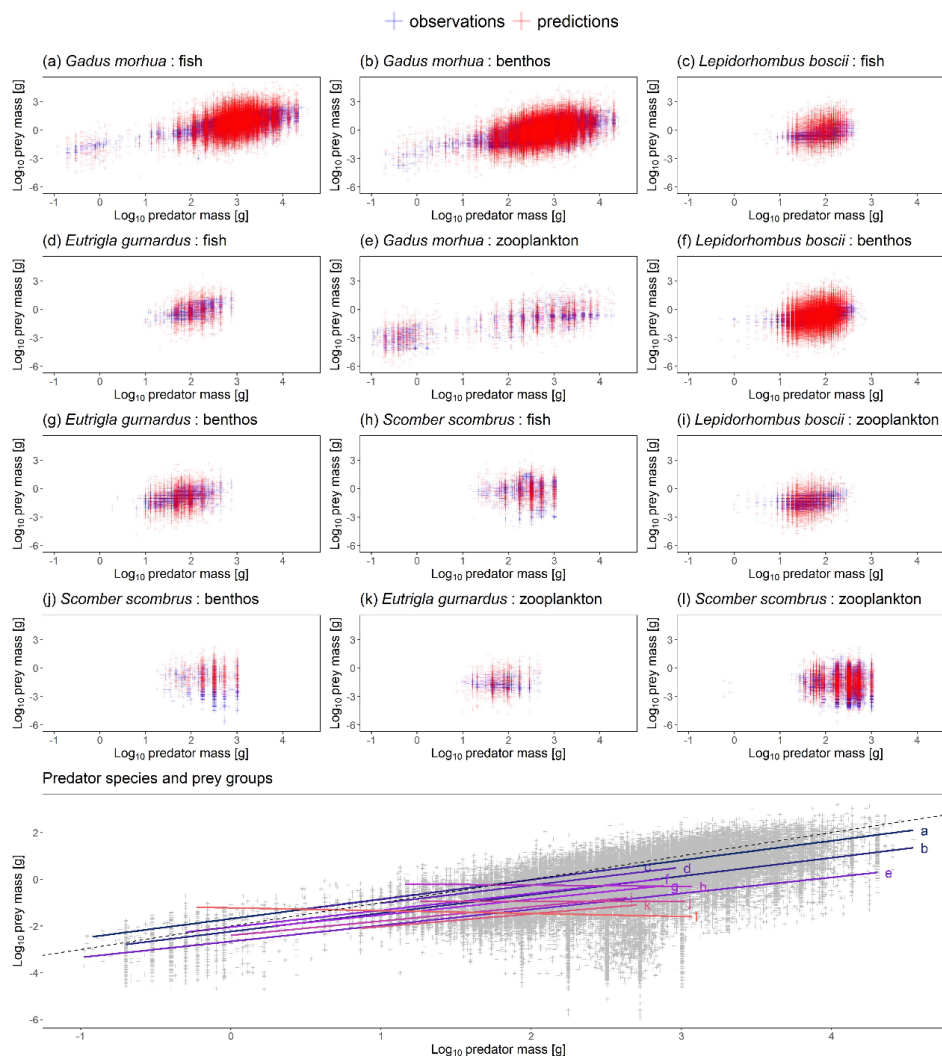
313 functional groups. Fish prey tended to be the biggest, meaning fish-fish interactions tended to have

314 higher intercepts and slopes (Fig. 3a, c, d, h) and thus the lowest mean PPMR, with predator species

315 of the same size consuming relatively small benthic and zooplankton prey (Fig. 3b, e, f, g, I, j, k, l).

316 These models enabled us to estimate prey biomass, counts and predator-prey mass ratios across the

317 different stomach contents datasets, species and size classes useful for feeding guild classifications

318 (Table S3).

319
320 Figure 3: A subset of the 498 unique combinations of predator species and prey functional group body
321 mass scaling relationships on log$_{10}$ transformed axes. Blue points = observed values for specific
322 relationships, red points = model predictions for specific relationships, grey points = all observed
323 values. The final plot 'Predator species and prey groups' shows the different scaling relationships
324 across the preceding plots, ordered by prey size at maximum predator size with a dashed 1:1 line to
325 show scaling relationships were generally sublinear (i.e., prey increased less than their predators per
326 unit increase in body size).
327

328 3.2 Feeding trait data reveal multiple distinct feeding guilds
329

330 Feeding guilds captured significant variation in the composition of predators for each cluster-based

331 method (Table 2), confirming our second hypothesis that multiple feeding guilds can be delineated

332   from the analysis of feeding traits. The occurrence method had the most robust feeding guilds with

333   the lowest compositional change in predators following re-sampling (mean distance to centroid =

334   0.13), followed by the trait (mean distance to centroid = 0.22) and then the biomass methods (mean

335   distance to centroid = 0.34; randomly generated feeding guild mean distance to centroid ranged

336   between 0.6 – 0.61; Fig. S2; Table S5). The trait method had the lowest sum of distances to the data

337   centroid (2,655 km) followed by the biomass (7,034 km) and occurrence methods (8757 km; Fig. S3).

338   The trait method was therefore preferred because it could identify multiple distinct feeding guilds

339   even where we consider small subsets of predator stomach contents (n = 30 stomach samples) while

340   being the least affected by spatial gradients in prey taxa.

341   The four feeding guilds identified using the trait method have been named based on the % biomass of

342   prey functional groups as follows: planktivores, benthivores, bentho-piscivores and piscivores (Fig. 4).

343   Differences between feeding guilds were related to predator size, which correlated positively with

344   piscivory and negatively with planktivory (Fig. S4). Small size classes of species often occur in the

345   planktivore guild, moving to another guild as they increase in size, with multiple medium- to larger

346   size-classes of a species often in the same guild (Table S3). Typically, the biggest fish within and across

347   feeding guilds had the highest PPMR (hence the sublinear relationship in Fig. 3, where prey increased

348   less than their predators per unit increase in body size), yet piscivores were typically the biggest and

349   had the lowest PPMR on average. This apparent contradiction is largely because small piscivores had

350   some of the lowest PPMR values, whereas big planktivores and benthivores had some of the highest

351   values (Fig. 4; Table S3).

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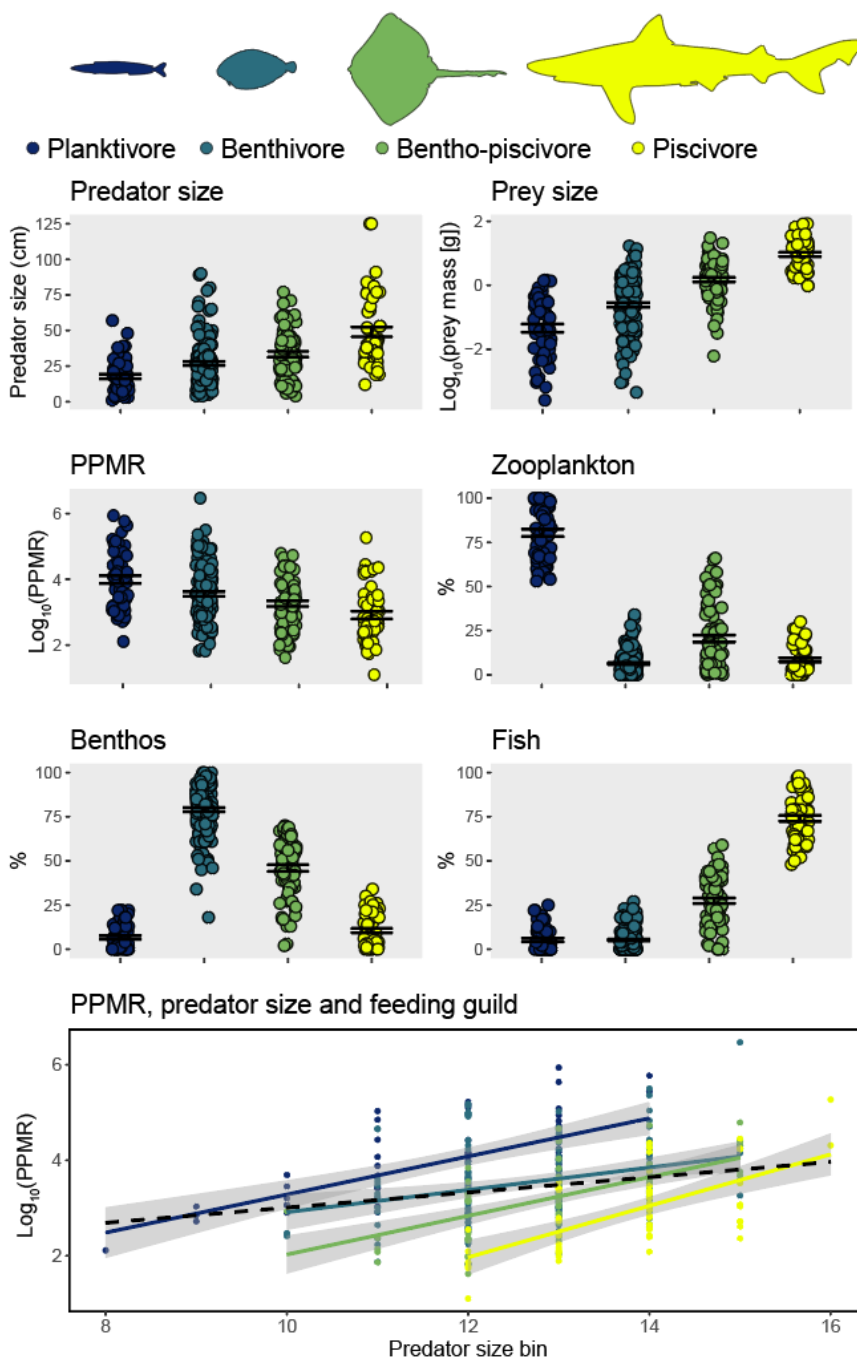
358   Table 2. Analysis of variance results across nested models for each cluster-based method and across
359   methods. Data for biomass, occurrence and trait methods were used to test whether guild (i.e.,
360   cluster-based groups) and data (i.e., a factor identifying each unique re-sampling event) captured
361   significant variation in the composition of predators. Data for all was used to test for differences
362   between the different methods (see also Table S5; Fig. S2). The term dropped column indicates which
363   term was dropped from each model (blanks indicate no predictors were dropped), AIC reveals change
364   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		
	Guild	3	-14526	592.83	<0.001
	Data	999	-15784	2.74	<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

365

366

367 Figure 4: Differences between feeding guilds in predator size, individual prey size, predator-prey mass
368 ratio (PPMR) and the % biomass contribution of different prey functional groups to stomach contents.
369 Points represent means for species size classes (Table S3), error bars represent standard error. Bottom
370 panel: PPMR increases with predator body size within (solid, coloured) and across (black, dashed line)
371 feeding guilds.

372   3.3 Feeding guilds capture significant spatiotemporal trends in survey data

373

374   When assigning feeding guilds in the survey data, we were able to classify 92% of the biomass which

375   included 122 species size classes. Many rare predators observed in the survey data (n = 366,

376   representing 8% of the surveyed biomass) remain unclassified due to insufficient stomach contents

377   data (Table S6). The perspective of change in the survey data is therefore weighted towards predators

378   contributing most to community biomass and ecosystem functioning. We found clear spatial structure

379   and regions of contrasting temporal change in feeding guild biomasses and their species richness (Figs.

380   5-6), confirming our third hypothesis. For instance, significant and spatially extensive temporal

381   decreases in planktivore feeding guild biomass lower in the food web were evident in the Celtic Seas

382   and Bay of Biscay where the biomass of the bentho-piscivore and piscivore feeding guilds higher in

383   the food web has increased (Fig. 5). Benthivore biomass has increased in the southern North Sea,

384   where there has been little change in other feeding guilds. Planktivore, bentho-piscivore and piscivore

385   biomass have all decreased in at least one assessment strata in the northern North Sea. Regions of

386   temporal change in species richness were also different across feeding guilds (Fig. 6). For instance,

387   over large areas in the Celtic Seas, Bay of Biscay and northern North Sea where there was relatively

388   limited change in planktivore species richness, the species richness of benthivores, bentho-piscivores

389   and piscivores all increased (see Fig. S5 for changes in unclassified biomass).

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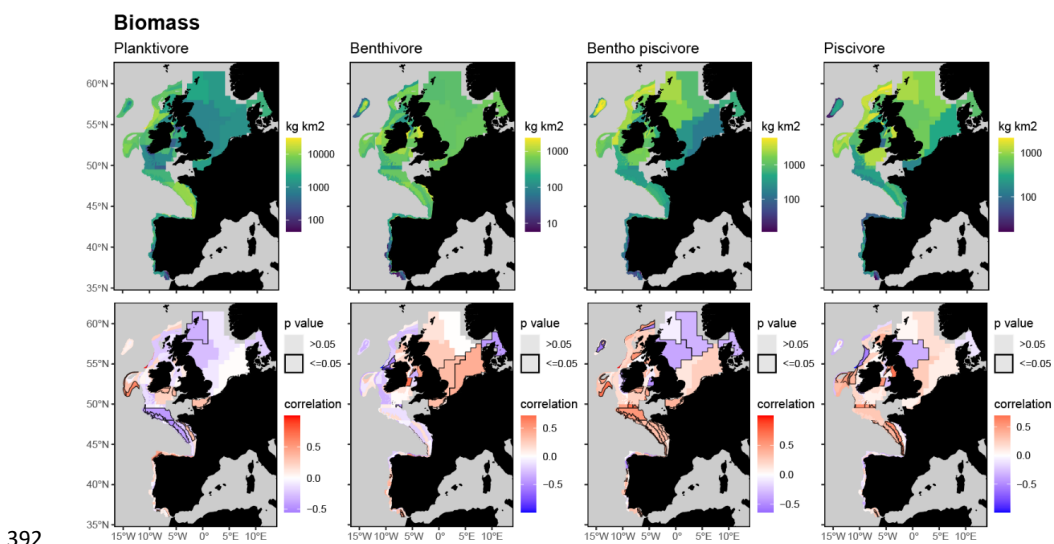
Figure 5: Mean spatial distribution (top row) and temporal change (bottom row) in feeding guild biomass by assessment strata based on otter trawl data. Significant temporal trends are highlighted with a black border and coloured blue or red to depict a decreasing or increasing trend, respectively (Kendall's τ scores of −1 to +1 represent a 100% probability of a decreasing or increasing trend).
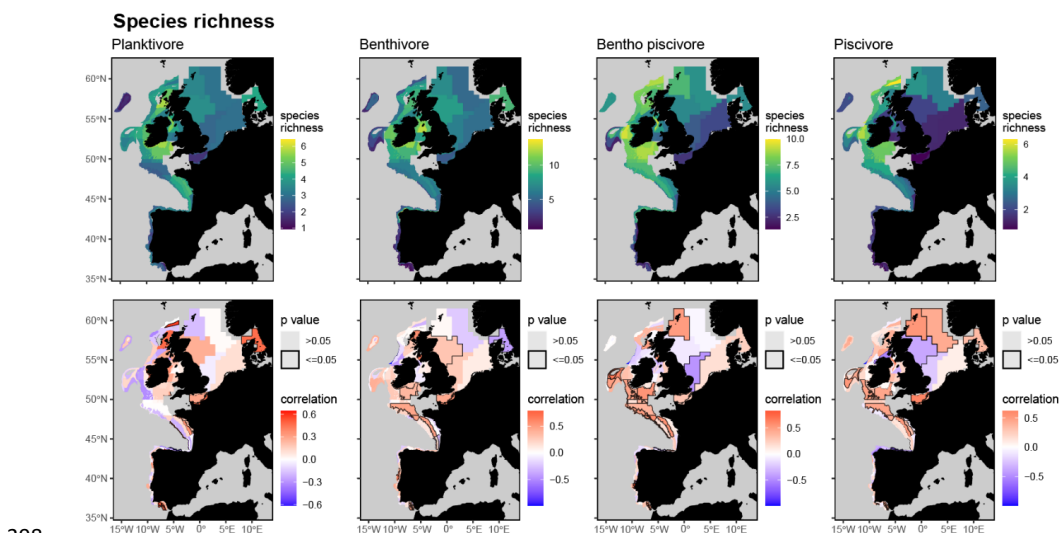
Figure 6: Mean spatial distribution (top row) and temporal change (bottom row) in feeding guild species richness by assessment strata based on otter trawl data. Significant temporal trends are highlighted with a black border and coloured blue or red to depict a decreasing or increasing trend, respectively (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 scaling models enabled predictions of mean individual prey mass for different predator species and prey functional groups across the Atlantic and Arctic Oceans. 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

432 estimates of predator-prey mass ratios, relative contributions of different prey groups, and from

433 multivariate analysis on the dissimilarity of species size class feeding traits (Table S3; Fig. S4) which

434 could help further unpick what such change means. This information is also widely applicable for

435 quantifying and predicting the effects of different fishing and climate regimes where changes in the

436 distribution of species and body sizes are anticipated (Kleisner et al., 2016; Lotze et al., 2019; Spence

437 et al., 2021; Thompson et al., 2023).

438 Previous studies which identified feeding guilds used differing approaches, relied on a subset of the

439 stomach contents data we use here and assessed different survey data to one-another (Garrison &

440 Link, 2000a, 2000b; Thompson et al., 2020). It was therefore not clear which method would be optimal

441 as an indicator across ecosystems. Moreover, differences in how feeding trait information has been

442 quantified and reported has hampered the synthesis of stomach contents data. Here, we brought

443 those different stomach contents data together by developing models to predict prey biomass and

444 counts where information was missing. We were then able to compare different approaches to

445 classifying feeding guilds across the datasets and apply the optimal approach to the same survey data.

446 This approach has helped achieve international consensus on how to assess feeding guilds across

447 ecosystems within the OSPAR Area (Thompson, Lynam, et al., 2023). The work we present here

448 represents a development of that pilot indicator, with improvements in how we estimated prey

449 weights (i.e., improved modelling framework that made use of more stomach contents data) which

450 affected feeding guild classifications; and the use of Kendall's τ trend analysis on the classified survey

451 data (as opposed to Pearson's correlation coefficients) in order to detect correlations which may be

452 non-linear. Many of the temporal patterns we present here are similar to those in the pilot indicator.

453 The most notable differences appear for feeding guild species richness where values were relatively

454 low (i.e., where relatively little change could have a large influence) in the central and northern North

455 Sea.

456 We use a trend-based assessment rather than one based on reference limits. Setting thresholds for

457 feeding guilds was outside the remit of this study and will require reference limits for Good

458   Environmental Status to be established. This could be done through synthesising empirical evidence

459   on feeding guild response to environmental change and human pressure (e.g., following Garrison &

460   Link, 2000b; Thompson et al., 2020) with dynamical modelling capable of predicting ecosystem state

461   under varying levels of human pressure (Link et al., 2010; Rossberg et al., 2017; Samhouri et al., 2010),

462   for instance. Such work would benefit from data products capable of integrating information from

463   different surveys, e.g., acoustic and various trawl gears, that catch a broad range of species and sizes

464   including smaller pelagic species which are likely under-sampled by demersal trawls (Kotwicki et al.,

465   2018; Nnanatu et al., 2020). Developing understanding of the drivers in spatial and temporal change

466   in fish feeding behaviour (Table S1) could also be fruitful, potentially leading to the quantification of

467   energy fluxes from different habitats (e.g., benthos and pelagic), regions, species, and seasons, for

468   instance. Such work could help develop understanding of the connections between the wider suite of

469   indicators which draw on different assemblages and often rely on data collected at different times and

470   at different spatial scales (e.g., Preciado et al., 2023). The inventory of feeding interactions could also

471   continue to develop, e.g., via surveys targeting areas and predators with limited information (e.g., Fig.

472   S5; Table S6), via DNA metabarcoding of stomach contents (Jakubavičiute et al., 2017), inference from

473   similar predators (Gray et al., 2015; Hicks et al., 2019), biotracers (Pethybridge et al., 2018) and

474   predictive modelling (Hernvann et al., 2022; Link, 2004; Petchey et al., 2008). Variability in digestion

475   rates driven by environmental gradients such as temperature and differences in prey sizes and tissue

476   composition could also be modelled to help improve estimates of biomass flux across the food web

477   (Temming & Herrmann, 2003).

478   Using change in functionally distinct feeding guilds to assess environmental status has been widely

479   advocated to fulfil OSPAR and the Marine Strategy Framework Directive requirements (Boschetti et

480   al., 2021; ICES, 2018; Rombouts et al., 2013; Tam et al., 2017; Walmsley et al., 2016), but international

481   consensus on how to do this has been lacking. We drew together data and expertise from across the

482   North Atlantic and Arctic Oceans to help achieve this. In doing so, we have made empirical estimates

483   of a range of key fish feeding traits that are widely applicable in marine ecosystem science, identified

484   robust feeding guilds, and revealed how and where ecosystem structure and function was changing

485   across the OSPAR Area. Such information will be critical to help better quantify and predict the effect

486   of human pressures, such as fishing and climate change, on global patterns in marine ecosystem

487   structure and functioning.

488

489   ## 5 Conclusions
490

491   We make use of multiple stomach contents databases to predict species- and size-specific feeding

492   traits for fish across the North Atlantic and Arctic Oceans. We then developed a repeatable, data-

493   driven workflow that categorises fish based on these feeding traits and show how they can be applied

494   to robustly define the feeding guilds required in OSPAR and the Marine Strategy Framework Directive

495   guidance. This has provided an indicator capable of revealing change in ecosystem structure and

496   function across the OSPAR Area based on routinely collected survey data. For instance, we reveal

497   significant and spatially extensive temporal changes across the food web, with decreases in the

498   biomass of smaller planktivorous fish which contrasted with increases in the biomass of larger more

499   piscivorous fish. The information we have generated can be tailored to fulfil other specific evidence

500   needs, such as improving the parametrisation of ecosystem models and quantifying sustainable levels

501   of human pressure. Our study provides evidence supporting a candidate food web indicator for the

502   OSPAR Area that can be readily extended to other areas and organisms.

503

504   ## 6 Competing interests
505

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

507

508   ## 7 Acknowledgements
509

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519   France-(Channel)-England cross-border European Cooperation Program, co-financed by the European

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521   VARITROPH project, funded by European Marine Fisheries Fund and France Filière Pêche

522

8 Authors' contribution statement

524
525   MSAT, CL, IP, AB conceived the project; MSAT, IP, VB, AB, MC, PC, EE, GH-M, IJ, FM, SR, SS, US, BES,

526   MAT and CL were involved in designing the methodology and collating the data; MSAT analysed the

527   data and led the writing of the manuscript. All authors contributed critically to the drafts and gave

528   final approval for publication.

529

9 Data availability

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532   The data we make use of are largely publicly available, cited, and displayed alongside URLs, where

533   applicable. We also provide all observed fish stomach contents data used in our modelling, predictions

534   of fish feeding traits from our linear mixed effects models, haul-level estimates of feeding guild species

535   richness, numbers of fish and their biomass based on scientific trawl surveys from the Northeast

536   Atlantic and the temporal trend values useful for indicator reporting processes

537   (https://doi.org/10.14466/CefasDataHub.149; Thompson et al., 2024).

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