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RESEARCH ARTICLE

A feeding guild indicator to assess environmental change impacts on marine ecosystem structure and functioning

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Abstract

1. Integrating food web indicators into ecological status assessments is central to developing effective management measures that can improve degraded ecosystems. This is because they can reveal how ecosystems respond to environmental change that cannot be inferred from studying habitat, species or assemblages alone. However, the substantial investment required to monitor food webs (e.g. via stomach contents analysis) and the lack of internationally agreed approaches to assessing them has hampered their development.
2. Inventories of trophic interactions have been collated world-wide and across biomes, and can be applied to infer food web structure and energy flow. Here, we compile a new marine dataset containing 8,092 unique predator–prey interactions from 415,294 fish stomachs. We demonstrate how feeding guilds (i.e. groupings based on diet and life stage) could be defined systematically and in a way that is conducive to their application internationally across ecosystems; and apply them to the North Sea fish assemblage to demonstrate their responsiveness to anthropogenic pressures.
3. We found evidence for seven distinct feeding guilds. Differences between guilds were related to predator size, which positively correlated with piscivory, phylogeny, with multiple size classes of a species often in the same guild, and habitat, as pelagic, benthic and shallow-coastal foraging was apparent.
4. Guild biomasses were largely consistent through time at the North Sea-level and spatially aggregated at the regional level with change relating to changes in resource availability, temperature, fishing and the biomass of other guilds. This suggests that fish biomass was partitioned across broad feeding and environmental niches, and changes over time were governed partly by guild carrying capacities, but also by a combination of covariates with contrasting patterns of change. Management of the North Sea ecosystem could therefore be adaptive and focused towards specific guilds and pressures in a given area.
5. *Synthesis and applications*. We propose a food web indicator which has been explicitly called for to inform policy via food web status assessment as part of the

European Union's Marine Strategy Framework Directive and the indicator toolkit supporting The Convention for the Protection of the Marine Environment of the North-East Atlantic (the 'OSPAR Convention').

KEYWORDS

ecological status assessment, ecosystem structure and function, environmental change, feeding guilds, fishing impacts, food web indicator, good environmental status, marine ecosystem

1 | INTRODUCTION

Determining how anthropogenic and environmental stressors affect ecosystems is critical in ecological status assessment. Analysis of food webs is seen as a key component in evaluating ecosystem status because they reveal system-level phenomena that cannot be detected by studying focal species or assemblages alone (Cohen, Schittler, Raffaelli, & Reuman, 2009; Rombouts et al., 2013; Tam et al., 2017). For instance, studies have shown that effects mediated via the food web can include changes to resources ('bottom-up' effects), to predation pressure ('top-down' effects), lead to secondary extinctions, and these responses, among others, may interact (Brose et al., 2017; Dunne, Williams, & Martinez, 2002; Lynam et al., 2017; Wang & Brose, 2018). In the marine environment, an area we focus on here, impacts from overfishing and warming associated with climate change have been widely reported to manifest at the food web-level (Ciannelli et al., 2007; Heath, 2005; Planque et al., 2010; Scheffer, Carpenter, & De Young, 2005). Hence, marine food web indicator development has received much recent attention (e.g. Greenstreet et al., 2011; Queirós, Fernandes, Genevier, & Lynam, 2018; Rombouts et al., 2013).

Organismal body size has been described as a 'super trait' since it determines many other traits which can affect food web structure and energy flux, such as trophic level, access to resources, vulnerability to predation and sensitivity to perturbation (Brose et al., 2006; Cohen et al., 2009; Hirt et al., 2018; Petchey, Beckerman, Riede, & Warren, 2008; Woodward et al., 2005). This has led to the use of body size distributions (e.g. Jennings, Pinnegar, Polunin, & Boon, 2001; Kerr & Dickie, 2001), such as proportion of large individuals (e.g. the large fish indicator; LFI; Engelhard, Lynam, García-Carreras, Dolder, & Mackinson, 2015; Greenstreet et al., 2011; Modica, Velasco, Preciado, Soto, & Greenstreet, 2014; Shephard, Reid, & Greenstreet, 2011), and the inclusion of species life stages to interpret changes to food webs (Clegg, Ali, & Beckerman, 2018). Research conducted by The European Science Foundation Research Network (SIZEMIC) indicated that further synthesis of taxonomic information with body size distribution data could help to develop a universal indicator of ecological status (Petchey & Belgrano, 2010). Despite this, and specific calls for the development of food web indicators within regulatory frameworks such as OSPAR and the Marine Strategy Framework Directive (MSFD), a more synthetic approach that encapsulates body size, taxonomy and feeding interactions has not yet been accepted into any indicator framework.

Using functionally distinct 'guilds' or 'groups' that encapsulate taxonomic and trait information relevant to food web assessment has been widely advocated (e.g. EC, 2010; ICES, 2014, 2018; Rombouts et al., 2013; Shephard, Greenstreet, Piet, Rindorf, & Dickey-Collas,2015). Yet, the process of defining such groups has received less attention, often relying on either feeding ecology, habitat preference, taxon-based morphological information or some expert judgement of a combination of these (e.g. Greenstreet, Bryant, Broekhuizen, Hall, & Heath, 1997; Heath, 2005; Reecht, Rochet, Trenkel, Jennings, & Pinnegar, 2013; Shephard et al., 2014; but see Garrison & Link, 2000a, 2000b). This makes comparisons across systems challenging because any difference could have a methodological basis. Another approach would be to comprehensively sur vey feeding interactions. However, this would be prohibitively expensive (Gray et al., 2015; Ings et al., 2009), especially given the dearth of feeding information for the lower tropic levels in marine food webs (Rombouts et al., 2013), and this is before more complex spatial and/or temporal changes in communities (e.g. via seasonal migrations) or interactions between small and large individuals are considered. Thus, despite the many potential advantages of food web assessment, and further integration of taxonomic and body size data into this, defining guilds and gathering feeding interaction data remains a significant challenge.

Inventories of trophic interactions with predator–prey body sizes have been collated world-wide and across biomes (e.g. Brose et al., 2005; Gray et al., 2015; Pinnegar, 2014). Information from these can be applied to assess within- and cross-system changes in food web structure and energy flow in a repeatable, standardized way. For instance, based on species lists collated during long-term UK-wide monitoring of running waters, Gray et al. (2016) used a feeding link inventory to infer food web structure and thereby asses biotic recovery following widespread improvements in water quality. Feeding inventories such as the 'Integrated Database and Portal for Fish Stomach Records' (DAPSTOM; Pinnegar, 2014) and ICES 'Year of the Stomach' database (ICES, 1997) https://ices.dk/data/data-portals/Pages/Fish-stomach.aspx exist for marine ecosystems but have not yet been applied to develop food web indicators. We combine these databases to produce the most comprehensive dataset of trophic interactions for the North East Atlantic (NEA) and its marginal seas. These data are then used to establish 'feeding guilds' (henceforth guilds, defined here as predators that have many prey taxa in common; Garrison & Link, 2000a, 2000b) for a range of juvenile and adult size classes per species using an approach that could be reproduced where taxonomic, feeding interaction and ontogenetic trait data exist. We then use these guilds to assess changes in fish populations in the North Sea as a case study. In doing so, our aim was to assess the applicability of guilds as the basis of an indicator for food webs to support OSPAR Quality Status Assessments (and fulfil the candidate indicator requirement 'biomass and abundance of functional groups') and Good Environmental Status assessments to meet the needs of the European MSFD and national reporting (e.g. UK Marine Strategy).

Specifically, we test for distinct guilds and partitioning of fish biomass across them, how this varies in space and time, and relate these to anthropogenic and environmental stressors. Because guilds integrate biomass structure with the processes that cause it, such as predation (e.g. variation in piscivore biomass), energy flux and resource limitation (e.g. via dynamic relations between guilds), recruitment and ontogeny (i.e. taxa occur across multiple guilds because their diet changes through ontogeny), we use the distribution and dynamics of guild biomasses as a measure of ecosystem structure and functioning. Hence, we assess whether change in the biomass of guilds in the North Sea was indicative of changes in ecosystem structure and functioning between 1985 and 2014, and whether adaptive management over that period (i.e. reductions in fishing activity) was detectable. We test the following hypotheses: (a) there are distinct guilds in the trophic interaction dataset; (b) guild biomasses, and thus food web structure and ecosystem functioning, vary in space; (c) spatiotemporal change in guild biomasses are related to changes in resource availability (bottom-up), temperature (which can be a combination of direct and indirect effects impacting both bottom-up and top-down processes, e.g. see Lynam et al., 2017), inter-guild predation and fishing (top-down effects). Our aim was two-fold: firstly, to develop a reproducible method for defining guilds and, secondly, to assess whether they could be applied to reveal ecosystem-level responses to stressors and thus offer potential as a food web indicator.

2 | MATERIALS AND METHODS

2.1 | Feeding guild classification

DAPSTOM is an ongoing initiative digitizing fish stomach records. The database contains information collected between 1836 and 2013 on 187 predator species (most occurring in northern European groundfish surveys). ICES Year of The Stomach Dataset contains records from 35 fish species between 1980 and 1991 sampled in the North Sea. Both datasets have information on predator–prey interactions for given sea areas and years. The new trophic interaction dataset spans the NEA (Figure S1), contains 8,092 unique predator–prey interactions from 415,294 fish stomachs, representing 155 predatory fish taxa and 1,643 prey taxa.

Guilds are defined here as a group of predators that have many prey taxa in common, and whose prey differentiate it from other predator guilds. We pooled all observed feeding links for five size classes of each predator taxa (usually predator species; predator groupings are thus referred to as taxa-by-size-classes) across both space and time to produce an aggregated diet for each. We pooled in this way because stomach contents analysis captures only a snapshot of a predator's diet, predators are typically gape-limited (i.e. body size is an important determinant of what prey are available to a predator), the developmental stage of fish is important for stock assessment and fishing is known to disproportionately remove large fish from high trophic levels (Greenstreet et al., 2011; Shephard et al., 2012; Shin, Rochet, Jennings, Field, & Gislason, 2005). Taxa-by-size-class categories were defined as: <3 cm considered larvae (Lv); small juvenile fish (Js) of 3 cm to half of length at maturity; juvenile-medium fish (Jm) from half of length at maturity to length at maturity; medium fish (M) from length at maturity to half-length at infinity and large fish (L) above half-length at infinity. Length at maturity and length at infinity were estimated for fish taxa using the r package Fishlife (Thorson, Munch, Cope, & Gao, 2017).

Any rarefaction to test for the number of stomachs required to reach a dietary asymptote would be confounded here by the differences in spatial and temporal distribution of sampling effort. For example, the number of samples required to classify the diet of a predator one year may be different from another year, or other predator species in the same year, simply because samples varied in their spatial distribution. Our aim therefore was to group fish into guilds based on their having similar predatory roles given the broadest understanding of predator–prey interactions and in a way that was insensitive to variation in sampling effort across predators. Hence, we selected only taxa-by-size-classes with 30+ stomach samples in the trophic interaction dataset to avoid inaccurate representation of diets. In addition, we use the presence of prey taxonomic 'family' to account for changes in predator–prey interactions through space and/or time, which will be strongly influenced by prey availability and sampling effort (e.g. Pinnegar, Trenkel, Tidd, Dawson, & Du buit, 2003; Woodward et al., 2010). Using prey species identity (e.g. rather than family) or a quantity (e.g. % occurrence) could mean we interpret predators to be selecting different prey and/or at different rates when in fact they are feeding on similar taxa at quantities driven by their relative abundance in the environment. An additional concern was that the diet width of predators with more stomach data could be broader due to sampling bias (e.g. Table S1). We attempt to standardize the data by using the median number of prey families exploited (n = 21) as a threshold for maximum diet width thereby excluding rarely consumed prey for highly sampled predators (i.e. to make sampling across predators more consistent, we use all data for the majority of predators, but remove rare prey from the minority of predators with the most data). We also distinguish fish larvae (≤3 cm) as prey from other fish (>3 cm), as feeding on larvae is analogous to zooplanktivory as opposed to piscivory, and use the lower taxonomic classification of 'order' for larvae due to the difficulty in resolving their taxonomy. Guilds were assigned in R using the stats package (R Development Core Team, 2018) and based on cluster analysis using the 'ward D2' agglomeration method on Sørensen dissimilarities on binary data. The optimum number of feeding guilds (i.e. clusters) was assessed using the average silhouette width (Kaufman & Rousseeuw, 2009), gap statistic (Tibshirani, Walther, & Hastie, 2001) and elbow method.

We explore differences between guilds by relating covariates to non-metric multidimensional scaling (nMDS) dimensions and generate p values based on n = 999 permutation tests using the *envfit* function in the R package vegan (Oksanen et al., 2015). Specifically, we assess whether variation in predator size, the occurrence of different prey functional groups (e.g. benthic, planktonic; using World Register of Marine Species classifications), prey types (after Pinnegar, 2014), prey phyla and variation in sampling effort across predators (i.e. number of stomachs) were significant explanatory variables in our ordination.

2.2 | Data and statistical modelling to assess changes in guild biomass and correlations with covariates

We investigate changes in biomass of guilds based on processed survey data (Moriarty, Greenstreet, & Rasmussen, 2017) and make use of the Greater North Sea otter trawl data in quarter 1 (i.e. the International Bottom Trawl Survey, henceforth trawl data; Moriarty & Greenstreet, 2017). We adjusted for the area swept to estimate the absolute biomass of each species and length category at the ICES statistical rectangle scale. Feeding guilds were allocated based on taxa and size category to estimate the annual biomass of each guild in each grid cell.

To estimate annual fishing pressure at the same scale, beam and otter trawl effort (fishing hours) was compiled for the period 1985–2014 after Couce, Schratzberger, and Engelhard (2020). Pelagic trawling impacts were estimated using landings reported by the Scientific, Technical and Economic Committee for Fisheries (2017). Annual estimates for pelagic landings for the complete guild biomass time series was not possible so only mean pelagic landings were assessed. As an estimate of resource availability, annual averages of zooplankton density were calculated for hydrodynamic regions (after Capuzzo et al., 2017; see also Van Leeuwen, Tett, Mills, & Van Der Molen, 2015) between 1985 and 2014 from the Continuous Plankton Recorder (CPR, https://www.cprsurvey.org/data/our-data/; Batten et al., 2003; SAHFOS, 2018). Mean annual sea bed temperature data were calculated using the data product published by the Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu) for the MyOcean project (see Wakelin et al., 2015).

We modelled annual estimates of fish biomass for the guilds at location s and time t (from 1985, t = 1, to 2014, t = 30), $\boldsymbol{G}_{s,t}$ (a 7-dimensional vector), as a function of top-down effects (beam trawl effort, $V_{\text{beam},s,t}$ and otter trawl effort, $V_{\text{otter},s,t}$), bottom-up effects (zooplankton abundance, $V_{\text{zoo},s,t}$ and pelagic fish landings, $V_{\text{pel},s,t}$) and temperature, $V_{\text{temp},s,t}$. To account for temporal and spatial correlation in the data, we used a mixed effect model (Figure 1).

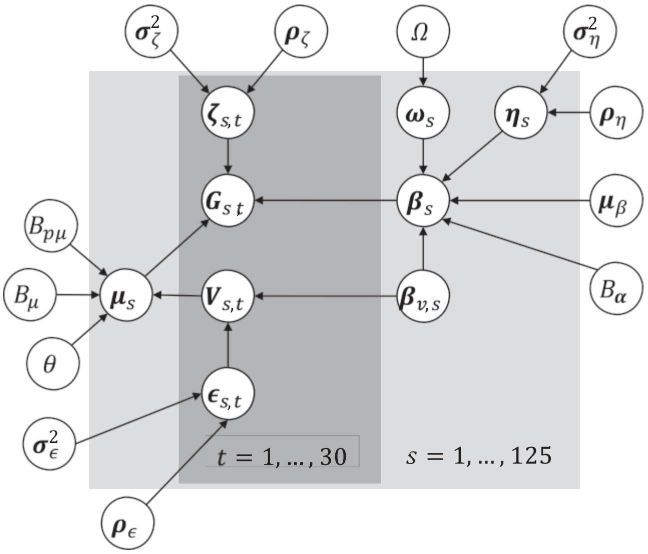

FIGURE 1 A directed acyclic graph of the model

For each location s, we calculated the mean value of the covariates across all 30 years,

$$\bar{V}_s = \frac{1}{30}\sum_{t=1}^{30} V_{s,t}, \tag{1}$$

where $V_{s,t} = (V_{\text{temp},s,t}, V_{\text{otter},s,t}, V_{\text{beam},s,t}, V_{\text{pel},s,t}, V_{\text{zoo},s,t})'$. For some of the covariates there was evidence of quadratic effects, $\bar{U}_s = \left(\bar{V}^2_{\text{temp},s}, \bar{V}^2_{\text{otter},s}, \bar{V}^2_{\text{beam},s}\right)'$. We defined the expected guild biomass at location s as

$$\mu_s = \theta + B_\mu \bar{V}_s + B_{p\mu} \bar{U}_s, \tag{2}$$

where θ is a 7-dimensional vector, B_μ is a 7 × 5 matrix and $B_{p\mu}$ is a 7 × 3 matrix. The dynamics of the covariates, $\boldsymbol{V}_{s,t}$, at location s and time t were described by

$$V_{s,t} = \bar{V}_s + t\beta_{v,s} + \epsilon_{s,t}, \tag{3}$$

where $\beta_{v,s}$ is a 7-dimensional vector and $\epsilon_{s,t}$ follows an independent auto-regressive model of order 1 (Chib, Omori, & Asai, 2009), i.e.

$$\epsilon_{s,t} \sim N\left(P_\epsilon \epsilon_{s,t-1}, \Sigma_\epsilon\right), \tag{4}$$

where the diagonal elements of P_ϵ and Σ_ϵ are ρ_ϵ and σ_ϵ^2 respectively, and the off-diagonal elements are 0. The rate of change in the guild biomass at location s was vector defined as

$$\beta_s = \mu_\beta + B_\alpha \beta_{v,s} + \eta_s + \omega_s, \tag{5}$$

where μ_β is a 7-dimensional vector, B_α is 7 × 5 matrix, η_s is sampled from a spatial auto-regressive model with correlation parameter ρ_η and variance a^2_1 (Ver Hoef, Peterson, Hooten, Hanks, & Fortin, 2018) and $m_s \sim N(0, \Omega)$. Ω describes the covariance of the rate of change between guilds. The guild biomass at location *s* and time *t* was

$$G_{s,t} = J._s + tp_s + \phi_{s,t}, \tag{6}$$

where Jl_s is the expected guild biomass at location *s*, defined in Equation 2, β_s, defined in Equation 5 and $\zeta_{s,t}$ follows an independent auto-regressive model of order 1 with parameters ρ_ζ and $o^2_{\{}$. Due to the dimensionality and correlation of the uncertain parameter space, we fitted the model using No U-turn Hamiltonian Monte Carlo (Hoffman & Gelman, 2011) in the R package STAN (Gelman, Lee, & Guo, 2015).

Using Bayes factors (ratios of the likelihood probability) we can evidence the relationship between the biomass of guilds and covariates in space and over time. We focus primarily on results which surpass the more stringent thresholds suggested by Gelman and Robert (2014; Bayes factors ≤0.04 and ≥25 indicate strong to compelling evidence for a negative or positive relationship, respectively) but note less compelling relationships following Kass and Raftery (1995) which could correspond with *p* values of 0.05 (Bayes factors between >0.04 to 0.333 and 3 to <25 indicate evidence for a negative and positive relationship, respectively).

We complement this finer spatial scale approach using structural change analysis (Zeileis, Kleiber, Walter, & Hornik, 2003; Zeileis, Leisch, Hornik, & Kleiber, 2015) to test for significant sustained temporal change in guild biomass at the whole system level. Further details of data generation and statistical modelling are given in Materials and Methods in Data S1.

3 | RESULTS

3.1 | Feeding guild classification

There were diet data for 220 taxa-by-size-classes (73 predator taxa) and multiple distinct guilds were evident (nMDS axes 1–2; $r^2 = 0.68$, $p = 0.001$; we selected seven as an optimum based on Figure S2), supporting our first hypothesis that multiple guilds are identifiable (Figure 2; Figures S3 and S4; Tables S1–S3). Omnivory was ubiquitous, with fish, benthic and planktonic prey occurring in the diet of all guilds, albeit to quite different levels. Arthropoda, specifically crustaceans, were the most frequently encountered prey phylum across all but a piscivorous guild (Table S2). Differences in the diet of guilds were related to the size of predators, which positively correlated with piscivory, and negatively correlated with % Annelida, Mollusca and Arthropoda, among other prey (Figure 2; Figure S4; Table S3). Differences between guilds were also related to habitat as, for example, planktonic and benthic foraging guilds were apparent, and these correlated with planktivory and benthivory gradients (i.e. predator clustering based on prey presence data was supported by the relative occurrence of prey functional groups to predator diets). The number of stomachs processed and the number of observations

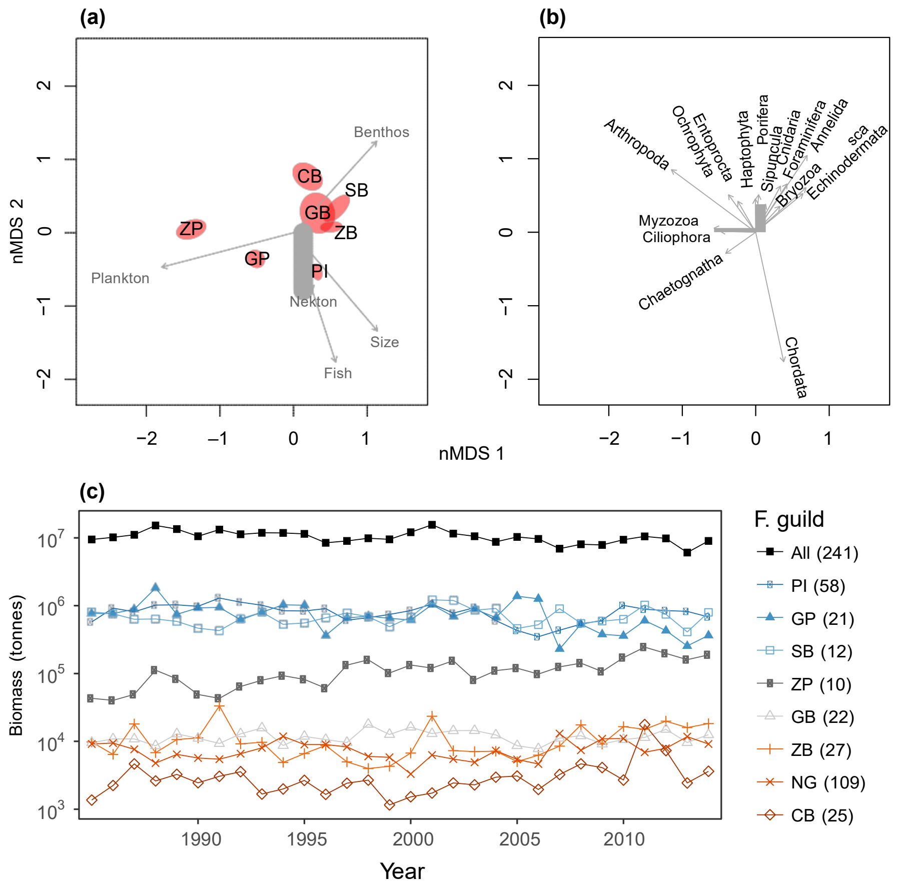

FIGURE 2 (a) Differences between guilds in nMDS represented by standard error ellipses with % occurrence of prey functional groups and predator length in cm (Size); (b) significant % occurrence of prey phyla recorded in predator stomach contents. (c) Variation in guild biomasses on a Log_{10} scale over the study period in the North Sea. CB, Coastal benthivore; GB, Generalist benthivore; GP, Generalist planktivore; NG, No guild; PI, Piscivore; SB, Specialist benthivore; ZB, Zoobenthivore; ZP, Zooplanktivore. The respective number of taxa-by-size-classes is represented in brackets

for each taxa-by-size-class were not significant explanatory variables for discriminating between guilds (Table S3), indicating that differences in sample size were not driving guild differences. The following seven guilds were identified: (a) 'Generalist planktivore'; (b) 'Zooplanktivore'; (c) 'Coastal benthivore'; (d) 'Generalist benthivore'; (e) 'Specialist benthivore'; (f) 'Zoobenthivore' and (g) 'Piscivore'. Guilds are described in detail in Results in Data S1.

3.2 | Guild-level assessment of North Sea Otter trawl data

All guilds identified in the NEA stomach contents data were present in the trawl data, with corresponding information for 175 taxa-by-size-classes representing 99.7% of the biomass (Figure 2; Tables S1 and S4). Three guilds made up 93.9% of the biomass: the Piscivore guild (33.6%) which was dominated by a range of whiting *Merlangius merlangus*, grey gurnard *Eutrigla gurnardus* and cod *Gadus morhua* size classes; the Generalist planktivore guild (31.1%) was dominated by juvenile herring *Clupea harengus*, followed by adult herring and a range of size classes of Norway pout *Trisopterus esmarkii* and mackerel *Scomber scombrus* (i.e. forage fish); and the Specialist benthivore guild (29.2%) contained a range of size classes of haddock *Melanogrammus aeglefinus*, dab *Limanda limanda*, plaice *Pleuronectes platessa* and sole *Soleo soleo*. The Zooplanktivore (4.7%), Generalist benthivore (0.5%), Zoobenthivore (0.5%), Coastal benthivore (0.1%), guilds represented a tiny fraction of the surveyed biomass (see also Results in Data S1; Table S4; Figures S5 and S6).

Guilds were widely distributed but their biomass was spatially aggregated within the North Sea, confirming our second hypothesis that ecosystem structure and function vary in space (Figure 3). The Piscivore and Zoobenthivore guilds aggregated in the west, Specialist and Generalist benthivore guilds in the north, the Coastal benthivore and Zooplanktivore guilds in the south, and Generalist planktivores were more patchy aggregating around Dogger bank and in the north, among other areas.

Guild biomasses related to environmental and anthropogenic covariates in space and over time, supporting our third hypothesis that resource availability, temperature and fishing effects are important drivers of change in ecosystem structure and function (Table 1; Table S5). The majority of guild and covariate spatial correlations were strong to compelling. For example, Piscivore guild biomass correlated positively with otter trawling, but negatively with pelagic landings, temperature and zooplankton density, and was not related to beam trawling; and otter trawling correlated negatively with Coastal benthivore biomass, with no relationship to Zooplanktivore biomass, and positively with all other guild biomasses (Figures 3 and 4).

Temporal correlations between guilds and between guilds and covariates were all weak. Temperature correlated dynamically and positively with Zooplanktivore biomass, and negatively with Generalist benthivore and Piscivore biomass. Zooplankton density correlated dynamically and positively with Zoobenthivore biomass. Negative dynamical relationships existed between beam trawling and Zoobenthivore and Piscivore biomasses highlighting potential negative impacts from fishing and recovery from it on these

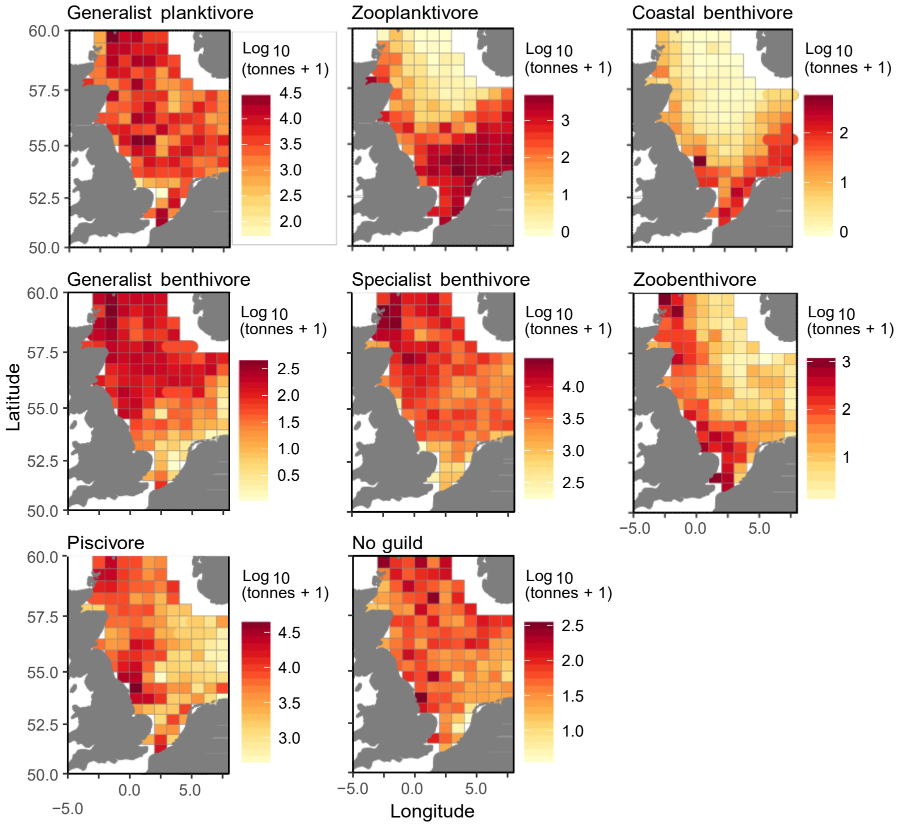

FIGURE 3 Mean feeding guild biomass distribution between 1985 and 2014 across ICES statistical rectangles in the North Sea

TABLE 1 Positive and negative relationships based on Bayes factors evident following mixed effect modelling for spatial (denoted by *) and dynamic correlations between guild biomasses and covariates. Columns represent guilds: GP = 'Generalist planktivore'; ZP = 'Zooplanktivore'; CB = 'Coastal benthivore'; GB = 'Generalist benthivore'; SB = 'Specialist benthivore'; ZB = 'Zoobenthivore'; PI = 'Piscivore'; related to covariates (rows). Compelling evidence for a negative (<0.01 = ---) or positive (>100 = +++) relationship; strong evidence for a negative (>0.01 to 0.04 = --) or positive (25 to <100 = ++) relationship; evidence of a negative (>0.04 to 0.333 = -) or positive (3 to <25 = +) relationship (see Table S5 for Bayes factors)

	GP	ZP	CB	GB	SB	ZB	PI
Temperature*	---	+++	+++	---	---	+++	---
Otter trawling*	+++		---	+++	+++	+++	+++
Beam trawling*	+++	+++	+	-	---	--	
Pelagic landings*	---		+	---	---	-	---
Zooplankton*	+++	+++	+++	---		---	---
Temperature		+		-			-
Otter trawling							
Beam trawling		+		+	+	-	-
Zooplankton						+	
ZP	+						
CB							
GB	+						
SB			+	+			
ZB				+	+		
PI	+		+	+	+	+	

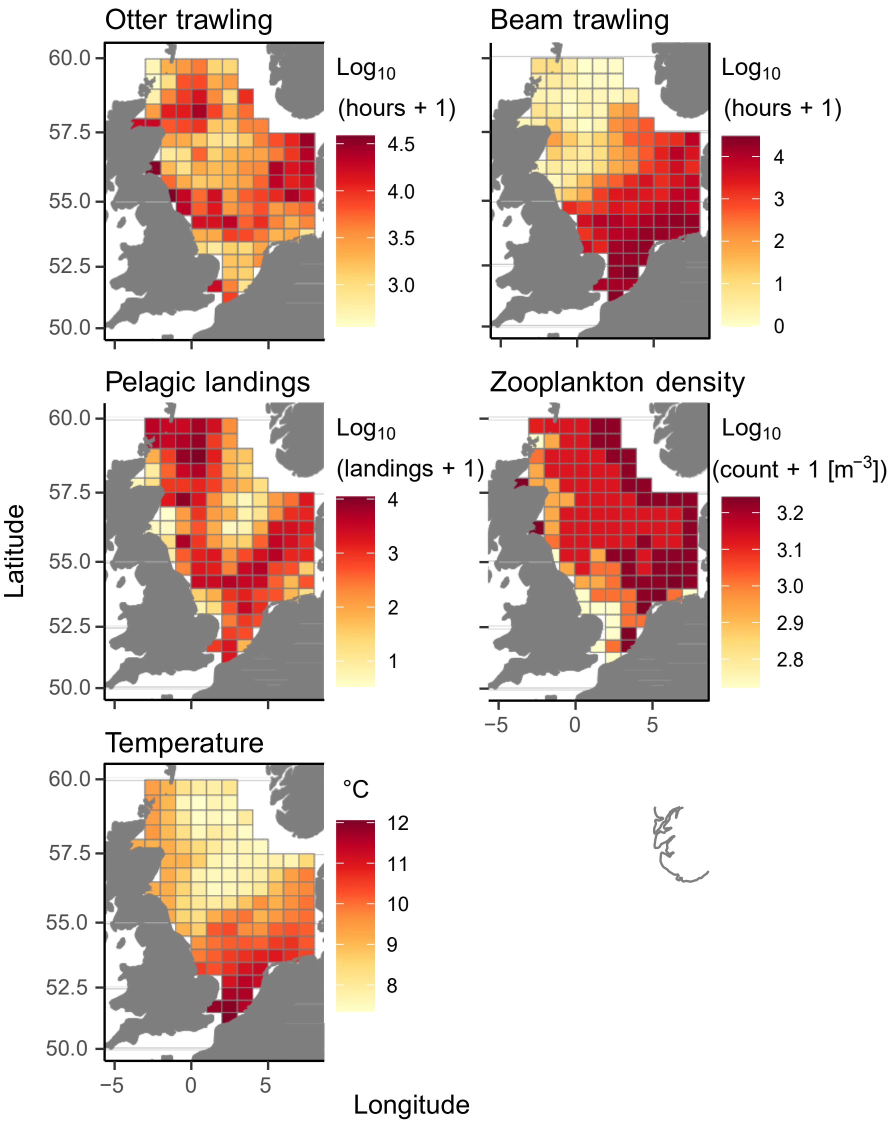

FIGURE 4 Mean covariate distributions between 1985 and 2014 across ICES statistical rectangles in the North Sea. Zooplankton density per m^3 has been calculated for hydraulic zones following Capuzzo et al. (2017)

guilds. However, weak positive dynamical correlations were also evident between beam trawling and Zooplanktivore, Generalist benthivore and Specialist benthivore biomasses (Figures 5 and 6). There was no evidence for negative dynamical correlations between guilds (i.e. top-down inter-guild control; Figure 5), but only weak positive correlations. Despite marked regional changes in guild biomasses (Figure 5) and large within-guild variation in the distribution of biomass between taxa-by-size-classes (Figure S6),

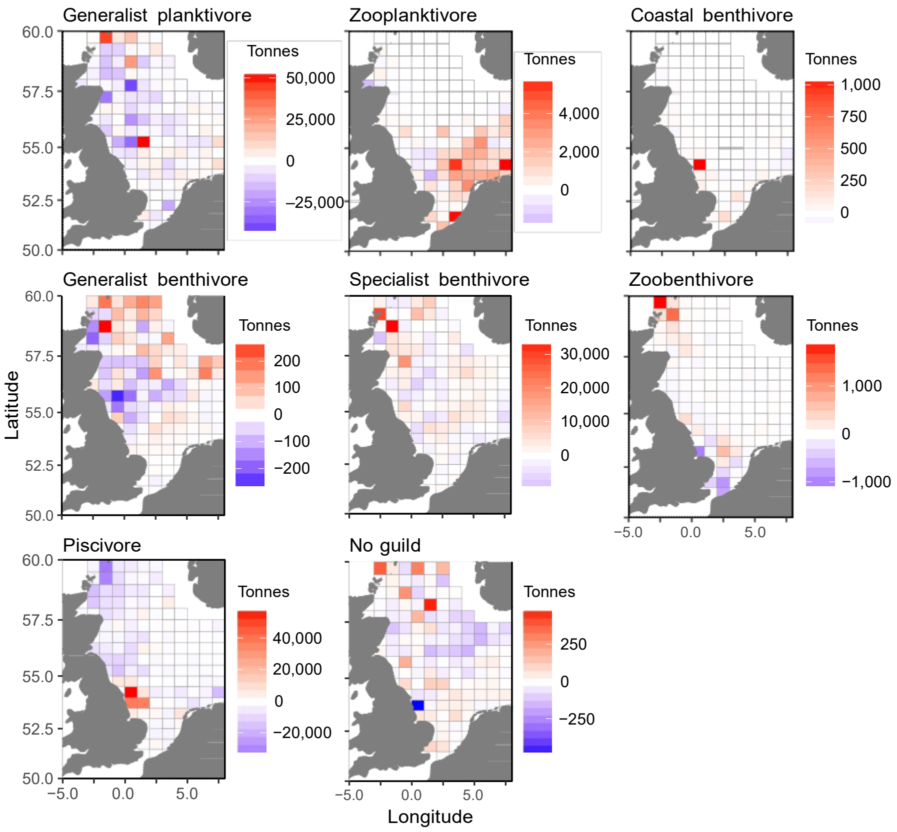

FIGURE 5 Feeding guild biomass change over time between 1985 to 1999 and 2000 to 2014 across ICES statistical rectangles in the North Sea

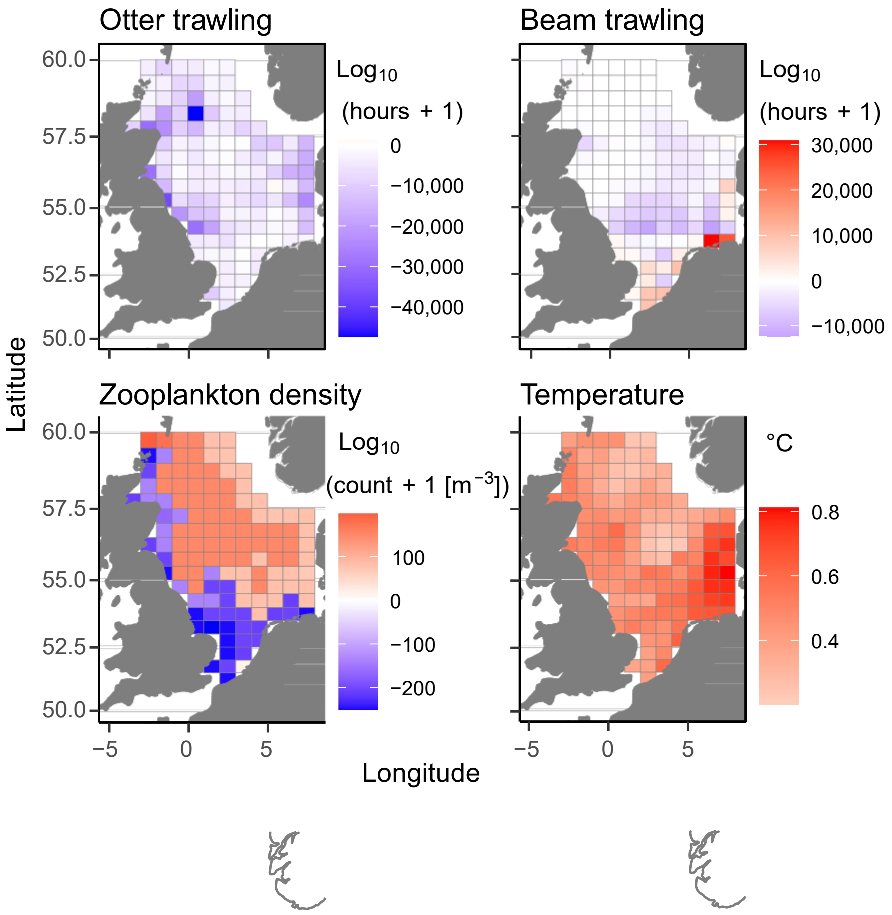

FIGURE 6 Change in mean annual fishing effort, zooplankton density and sea bed temperature (°C) between 1985–1999 and 2000–2014 across ICES statistical rectangles in the North Sea. Zooplankton density has been calculated for hydrodynamic zones following Capuzzo et al. (2017)

sustained changes at the North Sea scale were less apparent. Change in Zooplanktivore and Generalist planktivore guilds was driven by changes in the surveyed biomass of individual species within them, namely increasing juvenile sprat *Sprattus sprattus* and decreasing herring, respectively (Figure 2c; Figures S6 and S7), with shorter-term fluctuations evident in the Piscivore and Coastal benthivore guilds.

4 | DISCUSSION

Guild assessment represents a synthesis of taxonomic- and size-based approaches, supplemented with dietary information, that can reveal higher-level phenomena undetectable to its component parts if considered independently. For instance, temporal variation in Generalist benthivore and Piscivore guilds (Figure 5) was less apparent at the North Sea scale (Figure 2c) because of contrasting regional responses. Sustained changes were most apparent in guilds dominated in the survey by individual species. This highlights regional changes in food web structure and functioning but also points to guild carrying capacities. In studies of the fish community in the western Atlantic, Garrison and Link (2000a, 2000b) and Auster and Link (2009) found guild biomasses to be remarkably consistent through time despite fishery-induced perturbations on species within guilds. Given guild composition may change dramatically through time (Figure S6; see also Auster & Link, 2009; Garrison & Link, 2000a, 2000b) and in response to multiple drivers, guild biomasses were likely sustained via high functional redundancy analogous to the insurance hypothesis (Yachi & Loreau, 1999): whereby change in a species biomass is offset by contrasting change in another within the same guild such that guild biomass, which reflects the contribution of particular energy pathways to fish biomass, is relatively stable over time. Guild biomass is therefore likely constrained by the amount of available energy, the number of species able to exploit it, and changes to it highlight where pressures manifest at the system level. This, in turn, provides critical new insights into whether changes are caused by energetic constraints and/or environmental change, for instance, which is valuable information within the ecosystem approach to fisheries that could help to develop a more holistic understanding of anthropogenic impacts on ecosystems.

Our findings complement the powerful size-structuring widely reported to belie food web taxonomic structure (Brose et al., 2006; Clegg et al., 2018; Jennings, 2005; Jennings et al., 2001). For instance, fish with markedly different foraging strategies and evolutionary histories, e.g. dab, herring and saithe, grouped together as larvae and juveniles in the Zooplanktivore guild, but larger size classes of those species were grouped in different guilds suggesting divergence in foraging through ontogeny related to taxonomy and size, with many large apex predators in the Piscivorous guild. Moreover, the unique spatial distributions and unique correlations between each guild and the covariates suggests even apparently similar guilds, e.g. benthivores (Table 1; Figure 3), provide useful information about how foraging behaviour changes in space and over time. This highlights the complex interactions between species, size classes and diet embedded in the guild classifications which would not be considered if based on one or two of those components.

Our results show that the optimal number of guilds was between four and nine, with no clear threshold of change using the elbow method (Figure S2). We based our case study assessment on the North Sea using seven as an intermediate value but recognize a simpler or more complex approach could be justified and depends on the question. If the need was to understand relative changes in planktivory in its most simple form, the first split between planktivores and those more benthivorous and/or piscivorous in the dendrogram could be used (Figure S3). To get a more nuanced understanding of change with distinctions in the type of planktivory (e.g. specialist planktivores vs. zooplanktivores, the former of which preys on the latter) and benthivory (e.g. coastal vs. generalist) then more complex solutions would be justifiable. 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 organized. We provide a table in Data S1 which details the branches for up to nine feeding guilds so future assessments can choose which level of complexity suits their need (Table S6). And, because it is a data-driven, reproducible approach, new information can be systematically integrated to (a) further resolve the number of feeding guilds that can be confidently characterized, (b) their composition and (c) test if seasonal to annual changes in feeding behaviour provides evidence for dynamical classifications. Feeding interactions could, for example, be further spatiotemporally resolved by future targeted stomach content sampling (e.g. under-sampled taxa-size-class feeding interactions, Table S1) using conventional and emerging molecular techniques (e.g. see Pompanon et al., 2012), inferring from similar predators where species-level data are sparse (e.g. following Gray et al., 2015) and also via predictive modelling (Link, 2004; O'Gorman et al., 2019; Petchey et al., 2008).

Our mixed effect model and structural change analysis provide a 30-year overview of change at the ICES statistical rectangle scale with annual ecosystem-scale temporal dynamics, respectively. Stronger spatial rather than temporal effects were evident in the mixed effect model largely due to the level of change in space relative to change over time in both responses and covariates (Figures 3–6). For example, the spatial difference in mean annual temperature is ~4°C, whereas the largest change over time was ~0.8°C. By comparing findings across analyses we were able to better understand both the spatiotemporal scale and potential causes of change. For instance, Zooplanktivores showed a consistent increasing trend at the North Sea scale (Figure S7). Coupled with the results from the finer-scale assessment that shows a positive dynamical correlation with temperature (Table 1; Figures 5 and 6), this suggests Zooplanktivores (mostly juveniles of sprat and herring) were prospering where waters warmed most. Piscivores and Generalist benthivores did not show sustained declines over time despite having negative dynamical correlations with temperature. This is likely because of contrasting patterns of change in their biomasses with increases where warming was relatively low and decreases in coastal areas where warming was higher (Figures 5 and 6). Using the temperature-guild relationships evidenced here, future simulations could build on species-based approaches (e.g. Cheung et al., 2009), to make predictions about how ecosystem structure and function could be affected as warming becomes more pronounced.

The positive temporal correlations between guilds reported here could be caused by several factors potentially acting simultaneously: one guild received recruits from another, their resources and responses to environmental change were correlated and one or both consume the other without exerting top-down forcing. Since fishing fleets target adult size classes and can quickly adapt to spatiotemporal changes in target species biomass, the relationship between guild biomasses and fishing is also likely to be complex. For instance, positive spatial correlations between otter trawling and Specialist benthivore and Piscivore biomass were in line with our expectations. However, the negative spatial correlation between the Genralist planktivore guild and pelagic landings (used here as a proxy for fishing pressure on planktivorous fish; Engelhard et al., 2014), was not, possibly because juvenile biomass dominated this guild and the fishery targets adult fish across the Zooplanktivore and Genralist planktivore guilds which have contrasting distributions. Moreover, despite overall reductions in demersal fishing effort occurred during the study period (Figure 6; Couce et al., 2020), there was only weak evidence of negative impacts from fishing and recovery from it at the guild-level, possibly due to dynamic fleet behaviour and/or the long lag time expected for the recovery of fish communities (Fung, Farnsworth, Shephard, Reid, & Rossberg, 2013; Shephard et al., 2013). There were also likely indirect or spurious (i.e. coincidental) positive dynamical correlations between beam trawling and Zooplanktivore guild biomass. Given that we include juvenile and adult life stages across many fish taxa, there is potential for more complex guild-covariate spatiotemporal lags than was explored here. Future work could consider developing an approach to test for these more subtle but important lagged relationships and thereby further refine our understanding of responses to more heterogeneous and dynamic pressures such as fishing and resource availability (Fountalis, Dovrolis, Bracco, Dilkina, & Keilholz, 2018; Probst, Stelzenmüller, & Fock, 2012). To further understand how between-guild and guild-covariate correlations determine fish biomass distribution and their relative importance, future refinements could integrate acoustic survey data to better capture variation in pelagic fish populations and beam trawl survey data for benthic fish via Bayesian spatial multispecies modelling (e.g. Juntunen, Vanhatalo, Peltonen, & Mäntyniemi, 2012), for instance. Catchability corrections were not implemented here, but future research could estimate undersampling of some species due to behavioural responses (e.g. schooling, net avoidance) and/or limitations of the gear to catch particular size classes. Intra-guild indicators and synthesis with existing indicators would be another logical future development. A guild's size structure could be used to assess impacts from fishing via the Typical Length indicator (OSPAR, 2017a) or the 95% percentile of the length frequency distribution (Probst et al., 2012) and through change in species composition via the Mean Maximum Length Indicator (Fisher, Frank, & Leggett, 2010; OSPAR, 2017b). Measures such as intra-guild evenness and species richness could help to reveal key energetic pathways and the level of intra-guild redundancy. For example, we expect functional redundancy to be more constrained in guilds and areas dominated by a single species, hence where food web structure and ecosystem function are likely to vary most and be least resilient to change. And changes in total fish biomass, such as the decline ~2006 in the North Sea largely driven by the decrease in Generalist planktivore biomass, highlight the importance of particular guilds to system-wide structure and functioning (Figures S6 and S7). Developments such as these could therefore enable a more synthetic approach to understanding changes in ecosystem structure and functioning than has yet been achieved within the indicator framework.

Effective ecosystem management will need to consider how large-scale pressures, such as nutrient availability and temperature, and more localized and heterogeneous human activities, such as fishing, may interact (e.g. Capuzzo et al., 2017). In combination with a suite of indicators relating to species composition and size structure of communities, guild assessment could enable targeted advice for fishing-levels to offset impacts of increasing temperature and/or decreasing primary production, for instance, which cannot be managed directly in the short-term or locally. Comparable guild assessment could be applied in other marine systems (e.g. Garrison & Link, 2000a, 2000b) making the approach potentially applicable as part of a global-scale Integrated Ecosystem Assessment (DePiper et al., 2017). This will be informative to gauge how larger contrasts in environmental drivers, such as fishing and temperature, act on ecosystem structure and function, and thus enable a more predictive approach than was possible here. Moreover, the notion that, by supplementing organismal size with taxonomic information and feeding behaviour, the potential for a universal indicator of ecological status could be more rigorously tested.

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AUTHORS' CONTRIBUTIONS

M.S.A.T., H.P., M.A.S. and C.P.L. conceived the ideas and designed methodology; M.S.A.T., H.P., J.K.P., M.M., S.G. and P.H. collected the data; M.S.A.T., H.P., M.A.S., P.H. and C.P.L. analysed the data; M.S.A.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Processed interaction data are available from the Cefas datahub https://doi.org/10.14466/CefasDataHub.102 (Thompson et al., 2020). All other data used are cited and published.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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