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Research

Exploring the temporal variability of a food web using long-term biomonitoring data

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Ecological communities are constantly being reshaped in the face of environmental change and anthropogenic pressures. Yet, how food webs change over time remains poorly understood. Food web science is characterized by a trade-off between complexity (in terms of the number of species and feeding links) and dynamics. Topological analysis can use complex, highly resolved empirical food web models to explore the architecture of feeding interactions but is limited to a static view, whereas ecosystem models can be dynamic but use highly aggregated food webs. Here, we explore the temporal dynamics of a highly resolved empirical food web over a time period of 18 years, using the German Bight fish and benthic epifauna community as our case study. We relied on long-term monitoring ecosystem surveys (from 1998 to 2015) to build a metaweb, i.e. the meta food web containing all species recorded over the time span of our study. We then combined time series of species abundances with topological network analysis to construct annual food web snapshots. We developed a new approach, 'node-weighted' food web metrics by including species abundances to represent the temporal dynamics of food web structure, focusing on generality and vulnerability. Our results suggest that structural food web properties change through time; however, binary food web structural properties may not be as temporally variable as the underlying changes in species composition. Further, the node-weighted metrics enabled us to detect that food web structure was influenced by changes in species composition during the first half of the time series and more strongly by changes in species dominance during the second half. Our results demonstrate how ecosystem surveys can be used to monitor temporal changes in food web structure, which are important ecosystem indicators for building marine management and conservation plans.

Keywords: food web structure, temporal variability, topology

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Introduction

Ecological communities are constantly being reshaped by, for example, climate change and anthropogenic pressures either leading to losses (e.g. local extinctions) or gains (e.g. species invasions) in biodiversity (Pimm et al. 2014, Young et al. 2016). Additionally, species are connected through trophic interactions, and the presence or absence of a species may influence the dynamics of another through bottom–up or top–down control (Lynam et al. 2017). Food webs describe community composition and the trophic interactions among taxa. How food webs are structured is intimately related to the functioning of ecosystems and the services they provide (Thompson et al. 2012). Understanding how changes in species composition and trophic interactions affect the structure and functioning of ecosystems is of vital importance to guide ecosystem management and conservation (Cardinale et al. 2012, Thompson et al. 2012). Resilient ecosystem functioning is increasingly a focus of environmental legislation (Gray et al. 2014), and food web indicators constitute a component in assessments of 'Good Environmental Status' (European Union Directive 2008/56/EC). Yet, it remains unclear how the structure of food webs changes over time. Empirical studies remain scarce and heterogeneously scattered across realms, but highly encouraged (McCann and Rooney 2009, McMeans et al. 2015, Poisot et al. 2015, Saavedra et al. 2015, Ramos-Jiliberto et al. 2018, Ushio et al. 2018).

The challenges with temporal food web research are associated with the difficulty in monitoring food webs through time, i.e. recording the occurrence of all species and all of their interactions at each time step. The information required to assess changes in food webs over time has often been available only for smaller networks (such as the Skipwith pond food web, Warren 1989; the Elm flux or the Arctic tundra food webs, Schoenly and Cohen 1991), or more aggregated groups of species (North Sea Ecopath food web, Mackinson and Daskalov 2007), although aggregation is known to alter food web structure and to make comparability across studies questionable (Allesina and Bondavalli 2003, Pinnegar et al. 2005, Olivier and Planque 2017). Poorly and/or unevenly resolved dynamical food webs have also been used to investigate stability and food web dynamics (McCann 2000, Heath 2005), as well as management scenarios (Christensen and Pauly 1992, Ulanowicz 2004, Mackinson and Daskalov 2007). However, recent evidence suggests that the relationship between structural properties and stability can only be understood if multiple trophic levels and species interactions are considered at the same time (Soliveres et al. 2016, Seabloom et al. 2017, Barnes et al. 2018). Highly resolved food webs are seldom assessed using high-resolution temporal information. Temporal studies using highly resolved food webs and their topology often consider only a limited number of time steps, e.g. a before-and-after condition (Kaartinen and Roslin 2012, Yletyinen et al. 2016, Bodini et al. 2017). However, low temporal resolution may be insufficient to detect direction and strength of temporal changes. In our work, we explore long-term temporal variation in a highly resolved food web, adding a dynamic element to food web topology analysis.

Topological food webs portray the structure of trophic networks and can thereby encompass the large diversity of species and their interactions (Dunne 2009). Topological analyses are useful for summarizing structural properties of food webs and for comparing different ecosystems or regional food webs in space (de Santana et al. 2013, Wood et al. 2015, Kortsch et al. 2018). However, topological analysis of empirical food webs works under the assumption that food webs are static, although a recent study has shown that realized feeding interactions may be stochastic (Gravel et al. 2019). This static view neglects the spatiotemporal variability in species composition as well as rewiring of feeding interactions (McCann and Rooney 2009, Poisot et al. 2012, 2015), i.e. a change in interaction structure due to losses or additions of feeding links (Bartley et al. 2019). Empirical spatiotemporal variability in food web structure can come from distributional shifts of species following changes in the environment (e.g. thermal niche tracking, Beaugrand et al. 2014a, Hiddink et al. 2015, Weinert et al. 2016), such as the northward migration of cod seen in the Barents Sea (Kortsch et al. 2015). Generalist predator species react by adapting their sets of potential prey, ultimately leading to a topological rewiring of the food web (Thierry et al. 2011). Considering food webs as static has major influence on how we understand their structure and functioning. Therefore, in order to understand how changes in communities affect the structure of food webs, a framework that operates at the nexus of food web topology and dynamical food web models should be developed and applied (Thompson et al. 2012, McMeans et al. 2015).

Although it is challenging to monitor food webs over space and time, large amounts of data have already been collected that enable building spatiotemporally resolved food webs, e.g. monitoring of species composition, abundances and gut contents. From such data, it is possible to construct a metaweb – a food web which includes all species occurrences and potential trophic interactions at any given time and site within an area, e.g. the Benguela food web (Field et al. 1991). Based on the work of Havens (1992), Dunne (2006) showed that subsamples of a metaweb, also called food web snapshots, could provide spatiotemporal configurations of one food web solely based on which species co-occur. Kortsch et al. (2015, 2018) applied this technique to analyse the spatial variability of resolved, empirical marine food webs. A similar approach could be used to study temporal variability of food webs.

In the present study, we use standard topological analysis, on unweighted and weighted food web metrics (nodes weighted by species abundance), to explore and document temporal changes in food web structure. We investigated temporal variability of a marine food web by combining food web topology and time series analysis of species abundances. The 'node-weighted' food web metrics focused on aspects of generality and vulnerability, describing how many prey and predators, respectively, that species are connected to. We constructed a time series, spanning 18 years (1998–2015), of a food web for a small area in the German Bight (North Sea), which is monitored yearly. Using the monitoring data, we constructed a temporally resolved metaweb. We hypothesized that food web structure fluctuates over time due to changes in community composition following fluctuations in species abundances, likely as a response to large-scale changes in environmental conditions reported for the North Sea. For example, changes both in the physics (e.g. warming, Belkin 2009) and ecology for benthos and fish have been documented (e.g. climate-induced species migrations and distributional shifts, Perry et al. 2005, Neumann et al. 2013). Considering that both environmental conditions and ecological communities in the North Sea have changed, we could expect a temporal restructuring of the German Bight food web following changes in the occurrence of species. Therefore, our aim is to assess 1) whether and how food web structure has changed through time, and 2) how potential alterations are related to the composition and relative abundances of species.

Material and methods

Study area – time series of taxa abundances

The North Sea makes a good case study to investigate temporal changes in marine communities, as it has been well sampled over decades (Heessen and Daan 1996, Rijnsdorp et al. 1996, Ehrich et al. 2007). Numerous studies have documented the ecology and the dynamics of the system, e.g. community structure (Reiss et al. 2010, Sell and Kröncke 2013) and food web dynamics (Greenstreet et al. 1997). Furthermore, diverse stressors affect the North Sea (Emeis et al. 2015), including high fishing pressure (Daan et al. 2005) and climate change (Belkin 2009).

The effects of those stressors have channelled up from the population to the community level (Heath 2005). For the time period from the 1980s until the early 2000s, numerous studies have reported changes in species richness, abundance and community composition following, for instance, shifts in species distribution (Beaugrand 2004, Perry et al. 2005, Hiddink and Hofstede 2008, Kröncke et al. 2011, Simpson et al. 2011, Neumann et al. 2013, Weinert et al. 2016). Changes in the environmental conditions and in the community can be irreversible. A physical and biological regime shift was reported in the North Sea in the late 1980s (reviewed in Möllmann and Diekmann 2012) that altered the structure and trophodynamics of the fish community (Heath 2005). More recently, Dippner et al. (2010) and Beaugrand et al. (2014b) detected a biological regime shift characterized by changes in composition, abundance and biomass of plankton and benthic macrofauna in the late 1990s and early 2000s (Kröncke et al. 2013).

We used data collected through the German Small-scale Bottom Trawl Survey (GSBTS), a long-term, high-intensity sampling in selected small areas of 10 × 10 nautical miles (Ehrich et al. 2007). This survey monitors benthic epifauna and demersal fish. The benthic study is also part of Senckenberg's LTER North Sea Benthos Observatory. In our study, we focus on the area called 'Box A', located in the German Bight, at a depth of around 40 m. The GSBTS involves annual sampling of the demersal community during three consecutive days in summer (quarter 3), using an otter trawl at typically 21 stations (box coordinates and details available in Ehrich et al. 2007). The general methodology is the same as used for the large-scale International Bottom Trawl Survey (ICES 2015). The epifauna is sampled with a two-beam trawl at nine stations. This protocol has been carried out continuously since 1998 (no sampling was performed in 2013 due to a technical failure of the research vessel). Figure 1 outlines the area and summarizes the methodology of constructing temporal food webs explained below.

Species composition of the metaweb

We constructed a metaweb containing trophospecies (nodes) together with their trophic interactions. Our metaweb focuses on the benthic compartment of the German Bight, describing feeding habits of a subset of benthic epifauna and demersal fish recorded in the GSBTS. Trophospecies are groups of organisms (one or more species) that share the same predators and prey (Planque et al. 2014), and in our data set, they were always resolved to species level with the exception of seven aggregated functional groups: four primary producers (phytoplankton, microalgae, macroalgae, macrophyta), bacteria and detritus, as well as zooplankton, which may constitute the main resource for juvenile and pelagic fish. These functional groups were not sampled in the GSBTS, but included in the metaweb as they constitute important components of the marine food web. There was no further aggregation procedure applied to the species in the food web, and hereafter, we use the terms trophospecies and species interchangeably, as far as fish or benthic invertebrates are concerned.

In total, the GSBTS recorded 152 taxa of fish and benthic epifaunal invertebrates over the course of our study. However, the sampling effort varied between years and could potentially bias the observed occurrence of species. To select a constant number of sampling stations and to evaluate the sensitivity of our results to the inherent variability of the sampling procedure, we performed a bootstrap. We randomly selected 14 fish stations and seven epifauna stations per year and repeated this procedure 100 times.

To construct the metaweb, we selected taxa based on their persistence. We identified persistent taxa using the inflection points of the third-order polynomials fitted between the log of the total abundance and the number of years of presence, following Genner et al. (2004). The inflection points were detected at 10 and 11 years for fish and epifauna, respectively (Supplementary material Appendix 1 Fig. A1). We chose the most inclusive threshold, and thus included taxa detected at least 10 times (i.e. years) throughout the time series. The limited number of sampled stations may restrict

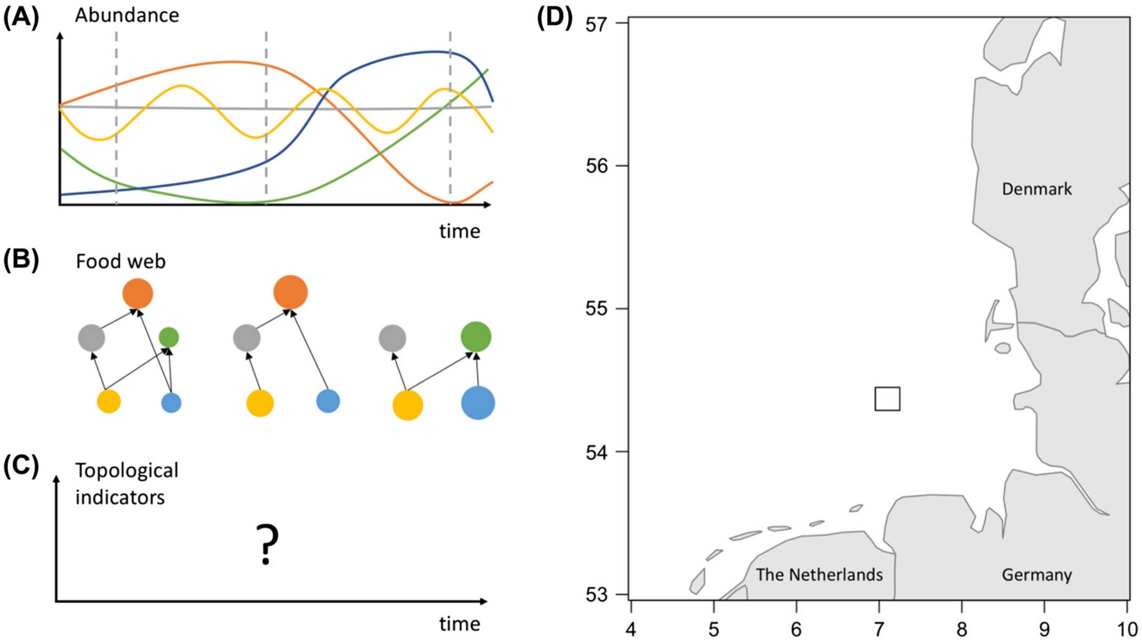

Figure 1. Schematic representation of the objectives of our study. (A) Temporal changes in abundance of species results in (B) changes in the topology of food webs that can be investigated with (C) time series of topological indicators. Our case study is (D) located in the German Bight, on a box of 10 by 10 nautical miles ('Box A' of the GSBTS), where fish and invertebrates have been sampled intensively for more than 18 years.

the detection of rare taxa. To test the sensitivity of our results to sampling intensity, we considered a three-year moving window that would include 35 fish and 17 epifauna stations. However, the results were coherent with the results based on the annual sampling data, but decreased the temporal resolution (Supplementary material Appendix 1 Fig. A4), and hence, the three-year moving window was rejected in favour of annual sampling data.

Some species may be abundant but not meeting the persistence criterion: for example, taxa that have a boom–bust dynamic (i.e. high abundances some years, below detection levels other years), taxa that have disappeared locally (i.e. are below detectable levels), or taxa that recently invaded the study area (i.e. now are above detection levels). However, given that the included taxa constituted 90% of the total abundance over the time series, we assume that we retained the most important species in the dataset (Supplementary material Appendix 1 Fig. A2). Time series of 'rare' (or poorly sampled) taxa are highly variable and unfit for deriving actual trends; therefore, 'rare' taxa were excluded from this study. Consequently, we chose not to assess the contribution of rare species to the temporal variability in food web structure, expecting minor influence of rare taxa on the abundance-related variability of food web metrics, but instead focused on core species and their interactions. In doing so, we excluded information on the temporal variability of part of the food web, likely resulting in conservative estimates of variability by focusing on the more stable core composition of the community.

In combining abundance data from the disparate fish and invertebrate surveys, we first calculated average abundance values for the 14 fish hauls and seven epifauna stations. To ensure comparability between iterations and sampling methods, the average abundance values were normalized using a logarithmic transformation and then divided by their global mean (i.e. total abundance divided by the product of the number of years and species), for fish and invertebrates, separately. This step brought fish and epifauna mean abundances to one. Abundances were sometimes lacking (e.g. for essential functional groups, such as 'phytoplankton'), and rather than removing these important taxa, we included them, but assigned them a constant abundance of one, which is the equivalent value of the normalized mean abundance for benthos and fish. Additionally, the trawl surveys did not quantitatively sample all taxa equally well. Pelagic fish were reported in the surveys, but their abundances are under-estimated using the otter trawl gear. To assess this uncertainty, we tested the influence of the abundance of pelagic fish on our results (i.e. using recorded abundances versus a constant abundance of one). We found that pelagic fish abundances affected food web metrics at the species level (e.g. node-weighted generality, see Supplementary material Appendix 1 Fig. A3). However, we kept the recorded abundances from the surveys, which is more realistic than assigning a constant value of one.

The taxonomy follows the World Register of Marine Species (WoRMS Editorial Board 2018) and is thoroughly described in the species list downloadable from the Dryad Digital Repository (Oliver et al. 2019).

Trophic relationships

Our metaweb represents a network of theoretically possible trophic interactions among taxa in the study area. We collected extensive data on the diet and feeding preferences of the selected species from literature and database records on trophic interactions, such as GloBI (i.e. Global Biotic Interactions, Poelen et al. 2014), which includes e.g. peer-reviewed literature on food webs (Raymond et al. 2011) and stomach content analysis (Pinnegar 2014). The full procedure for link determination is available in the Supplementary material Appendix 2 Section 1.

We assumed that trophic interactions documented in years outside our time series, or in areas outside the North Sea (e.g. reported 50 years ago, or for the Celtic Sea), were also possible interactions for the years we focused on and in the study area. However, co-occurrence of species is not evidence of trophic interactions (Cazelles et al. 2016, Freilich et al. 2018). A metaweb relying on temporally and spatially cumulative information, as in our study, likely overestimates the number of links realized at any given time and, therefore, also leads to overestimation of structural metrics, such as link density, generality and vulnerability. Hence, the metaweb represents a possible set of interactions for the benthic community in the German Bight study area.

In assigning trophic interactions, we excluded any ontogenetic diet shifts – making no distinction between a juvenile and an adult, and not assigning feeding preferences for different life stages – which may have led to an average lower trophic positioning of taxa than reported using e.g. stable isotopes (Silberberger et al. 2018). Some taxa feed on the eggs and larvae of other taxa (e.g. adult herring feeding of cod eggs and larvae). As we excluded ontogenetic diet shifts, these consumers would also be assumed to feed on the adult life stages; therefore, feeding on larvae or eggs was excluded.

Information on trophic interactions is biased towards predators and commercial species (e.g. cod), which are often more intensively studied compared to less common species or invertebrates. Indeed, most trophic interactions originate from observations of predators' diet (e.g. stomach content analysis and feeding experiments), and the higher the trophic level, the more detailed the reported information. Although we tried to build the most complete metaweb for the study area, information for some taxa was still lacking. To solve this problem, we inferred links by assuming that taxonomically related species with similar characteristics (e.g. morphology) may share predators or have similar diets (Laigle et al. 2018). This may overestimate the number of realized links and likewise overestimate food web metrics such as link density, generality and vulnerability. However, any trophic links inferred (e.g. based on taxonomic relatedness, or observations at different time periods or in different regions) were subsequently assessed by taxonomic experts on these species (see Supplementary material Appendix 2 Section 2 for the expert check procedure). The proportion of inferred links (31%) is comparable to other published food webs, such as for the Barents Sea (Planque et al. 2014). When selecting species using the persistence criterion, three predator nodes (*Acteon tornatilis*, *Macropodia rostrata*, *Nymphon brevirostre*) ended up with no resources (prey) included in the metaweb. These predators were removed from our data set as they are not correctly represented without prey in the food web.

The metaweb, including all diet references, can be downloaded from the Dryad Digital Repository. The metadata are also thoroughly described in the Supplementary material Appendix 2 Section 3.

Analysis and food web descriptors

We combined topology analysis with time series analysis to identify changes in the community structure. At each time step, we subsampled the metaweb according to the presence/absence of species within a given year. To identify changes in food web structure, we chose complementary and widely used food web metrics: species richness of the food web (S), linkage density (Z), directed connectance (C), generality (G), normalized standard deviation in generality (GenSD), vulnerability (V), normalized standard deviation in vulnerability (VulSD), mean short-weighted trophic level (TL) and mean maximum trophic similarity (MxSim). The formulas, together with definitions and primary references for each metric, are listed in Table 1.

To investigate the impact of fluctuations in species abundances on food web properties, we additionally calculated two metrics, node-weighted generality and node-weighted vulnerability, by weighting the binary link distributions using species abundances. Unlike traditional ways of weighing food web metrics based on energy flow between taxa (Bersier et al. 2002), we included information on the abundance of species to the nodes. In doing so, we considered each species as an aggregate of individuals expressing the same potential interactions. Each individual of each species, and their trophic links, are thereby considered nodes and links in the network. Changes in species abundances are thus reflected in the dynamics of node-weighted indicators of the food web.

As the weighted metrics in our study are weighted by abundances of species assigned to the nodes of the species, and not the links, we call them 'node-weighted metrics'. We defined node-weighted generality (wG) as the average number of prey by predator weighted by the abundance of predators, as described in eq. 1:

$$\mathrm{wG} = \frac{\sum_{k=1}^{j}\left(w_k \sum_{i=1}^{S}\left(a_{ik}\right)\right)}{\sum_{k=1}^{j} w_k} \qquad (1)$$

where *k* can be any of the species (*S*) in the food web, *i* and *j* are the prey and predators, respectively, and *wk* the

Table 1. Selected food web metrics and their definition. ‘L’ denotes the number of trophic links in the food web, S the number of species or species richness of the food web, *k* can be any trophospecies, w_k the abundance of trophospecies *k*, a_{ik} is a prey *i* in the diet of predator *k* (and conversely for a_{kj}), n_i and n_j are the number of prey and predators, $\mathbf{sim}_{ij}$ is the weighted mean of the Jaccard similarity of prey (weight of 0.4) and predators (weight of 0.6) between species *i* and *j*.

Metric and formula	Definition and references	Ecological implications
Linkage density $Z = L/S$	Number of interactions per taxa (Dunne 2009)	Z informs on how connected species are within the network
Directed connectance $C = L/S^2$	Proportion of all possible trophic links (S^2) that are realized (Dunne 2009)	A measure of network complexity that relates to the robustness of food webs in the face of perturbation
Generality $G = \frac{\sum_{k=1}^{j} a_{ik}}{n_j}$	Mean number of prey per predator (Schoener 1989)	Indicates if the system contains more generalist or specialist species
Node-weighted generality $\mathrm{wG} = \frac{\sum_{k=1}^{j}\left(w_k \sum_{i=1}^{S}\left(a_{ik}\right)\right)}{\sum_{k=1}^{j} w_k}$	Abundance-weighted mean of the number of prey per predator (this study)	Indicates if the system contains more generalist or specialist species, based on predator abundances
Normalized standard deviation in generality $\mathrm{GenSD} = \sqrt{\frac{1}{S-1}\sum_{k=1}^{S}\left(G_k - \overline{G_k}\right)^2}$ where $G_k = \frac{1}{Z}\sum_{k=1}^{S} a_{ik}$	Dispersion in the normalized generality (Williams and Martinez 2000, Bersier et al. 2002)	Reflects the variability in the number of prey per predator
Vulnerability $V = \frac{\sum_{k=1}^{i} a_{kj}}{n_i}$	Mean number of predators per prey (Schoener 1989)	Indicates the degree to which species function as prey
Node-weighted vulnerability $\mathrm{wV} = \frac{\sum_{k=1}^{i}\left(w_k \sum_{j=1}^{S}\left(a_{kj}\right)\right)}{\sum_{k=1}^{i} w_k}$	Abundance-weighted mean of the number of predators per prey (this study)	Indicates the degree to which species function as prey, based on prey abundances
Normalized standard deviation in vulnerability $\mathrm{VulSD} = \sqrt{\frac{1}{S-1}\sum_{k=1}^{S}\left(V_k - \overline{V_k}\right)^2}$ where $V_k = \frac{1}{Z}\sum_{k=1}^{S} a_{kj}$	Dispersion in the normalized vulnerability (Williams and Martinez 2000)	Reflects the variability in the number of predators per prey
Mean short-weighted trophic level $TL = \frac{\sum TL_k}{S}$ where $TL_k = 1 + \frac{\sum_{i=1}^{S} TL_i}{n_i}$ and TL_i represents the trophic level of each prey, and a consumer *k* is assumed to consume all its prey equally	Mean of the prey-averaged trophic level calculated from the shortest path between a taxon and a basal species (Williams and Martinez 2004, de Santana et al. 2013)	Lower TLs indicate a more energy-efficient system with fewer steps between a taxon and a basal species
Mean maximum trophic similarity $\mathrm{MxSim} = 1/S\sum_{i=1}^{S} \max \mathbf{sim}_{ij}$ with $i \neq j$	Mean maximum similarity of shared predators and prey, measured as the weighted Jaccard similarity index (Olivier and Planque 2017, following Williams and Martinez 2000)	A high value shows that most consumers feed on the same resources, which may indicate low food partitioning and higher competition in the system
Dissimilarity in species composition $\beta_S = \frac{a+b+c}{(2a+b+c)/2} - 1$ where *a* is the number of species in common between two food webs, *b* the number of species unique to the first food web and *c* the number of species unique to the second food web	Dissimilarity in species composition between two food webs (from Poisot et al. 2012, and based on beta diversity β_w by Whittaker 1960)	Indicates how the species composition differs between food webs
Dissimilarity in trophic interactions due to species turnover $\beta_{ST} = \frac{a+b+c}{(2a+b+c)/2} - 1$ Considering only common species between two food webs; *a* is the number of common trophic interactions, *b* the number of unique interactions to the first food web and *c* the number of unique interactions to the second food web	Dissimilarity in interactions of common species between two food webs (from Poisot et al. 2012, and based on beta diversity β_w by Whittaker 1960)	Indicates how food webs differ in trophic interactions due to turnover in species composition

abundance of a species. Node-weighted generality is thus the number of prey per predator, weighted by a predator's relative abundance. Similarly, for prey taxa, we define node-weighted vulnerability (wV), as described in eq. 2:

$$\mathrm{wV} = \frac{\sum_{k=1}^{i}\left(w_k \sum_{j=1}^{S}\left(a_{kj}\right)\right)}{\sum_{k=1}^{i} w_k} \tag{2}$$

When calculating node-weighted generality and node-weighted vulnerability, nodes are weighed by the abundances of the species. As our fish and benthic epifauna abundances were normalized, we, here, used the exponential of the normalized abundance to highlight differences among species (exp − 1).

All nine food web metrics were presented as annual median values based on the bootstrap of the constant sampling effort. To help visualize the temporal fluctuations of the metrics, we applied a LOESS smoothing (span = 0.75) to the median values of the time series.

To visualize changes in underlying community composition, we used heatmaps representing anomalies of abundance fluctuations, calculated as standardized abundance (difference between annual value and the average value divided by the standard deviation). Anomalies going from positive to negative represent declines in abundances. Trends going from negative to positive anomalies represent increases in abundances.

Finally, we estimated the temporal β-diversity between pairs of food web snapshots – the temporal turnover in species composition β_S and in trophic interactions due to species turnover β_{ST} – using the betalink package in R (Poisot et al. 2012, Kortsch et al. 2018). Dissimilarity of species interactions depends on turnover in species composition and realized interactions (i.e. rewiring of interactions). In our case, β-diversity of species interactions depends solely on turnover in species composition, because

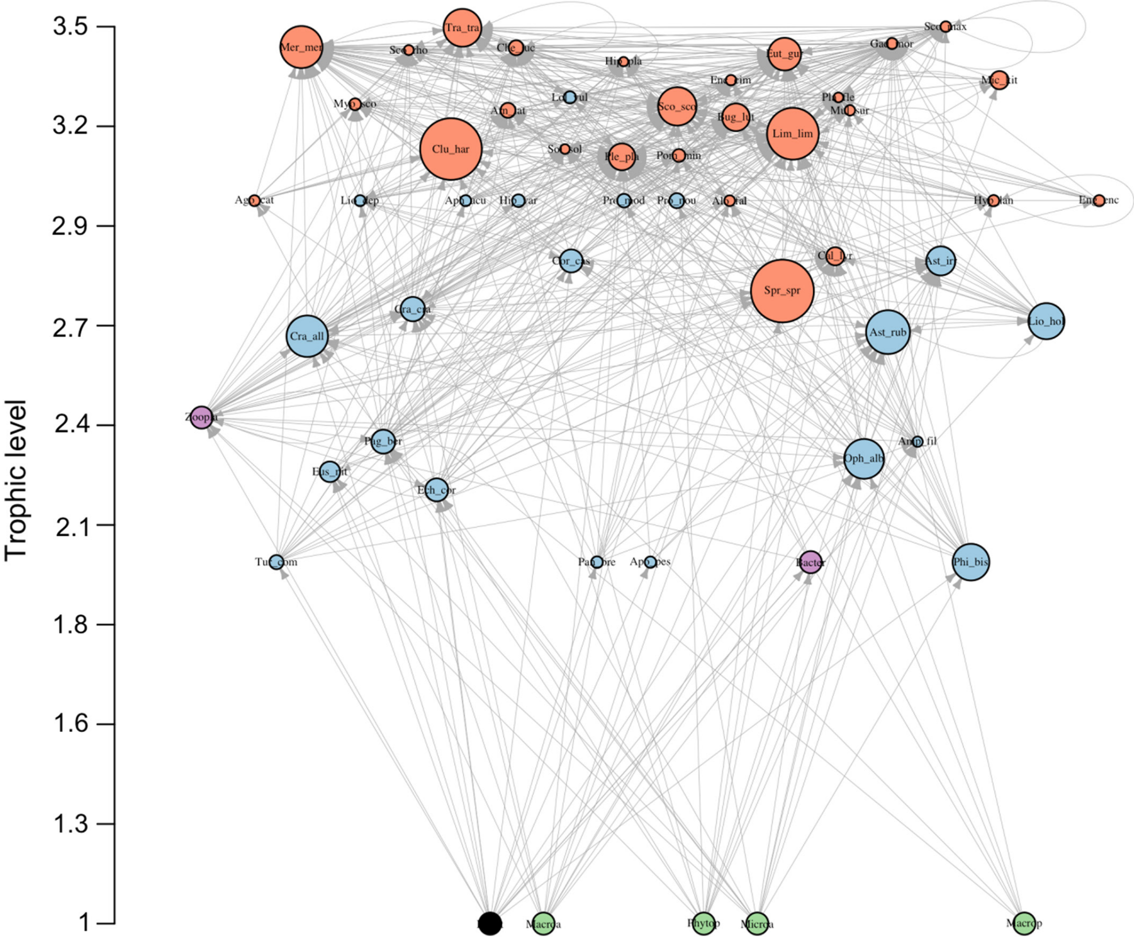

Figure 2. Metaweb of the German Bight. The y-axis indicates the trophic levels of the species. Basal species are represented at the bottom and connected to higher trophic level by trophic links (i.e. arrows directed from the prey to the predator). The size of the nodes is proportional to the mean log-transformed abundance of species over the 18-year time series. Name abbreviations identify species in the species list. Red, blue, purple, green and black nodes represent fish, invertebrates, grazers with constant abundance, primary producers and detritus, respectively.

our temporal food webs were subsampled from a metaweb, which likely results in lower estimates of dissimilarity of interactions. All data analyses were performed with the statistical software environment R (R Core Team) and food webs were visualized using the 'igraph' R package (Csárdi and Nepusz 2006).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9tg3t75> (Olivier et al. 2019).

Results

The metaweb

To investigate temporal changes in the structure of a marine food web, we built a metaweb that contains 55 trophospecies (S) selected out of 152 taxa in the original GSBTS data set. The metaweb contains 588 trophic links (L) divided between 21 epifaunal invertebrates and 27 fish taxa resolved to species level, and the seven functional groups (Fig. 2). The link density (Z) is 10.7 links per node and the connectance (C) is 0.19, i.e. the food web expresses 19% of all possible trophic interactions. The annual food

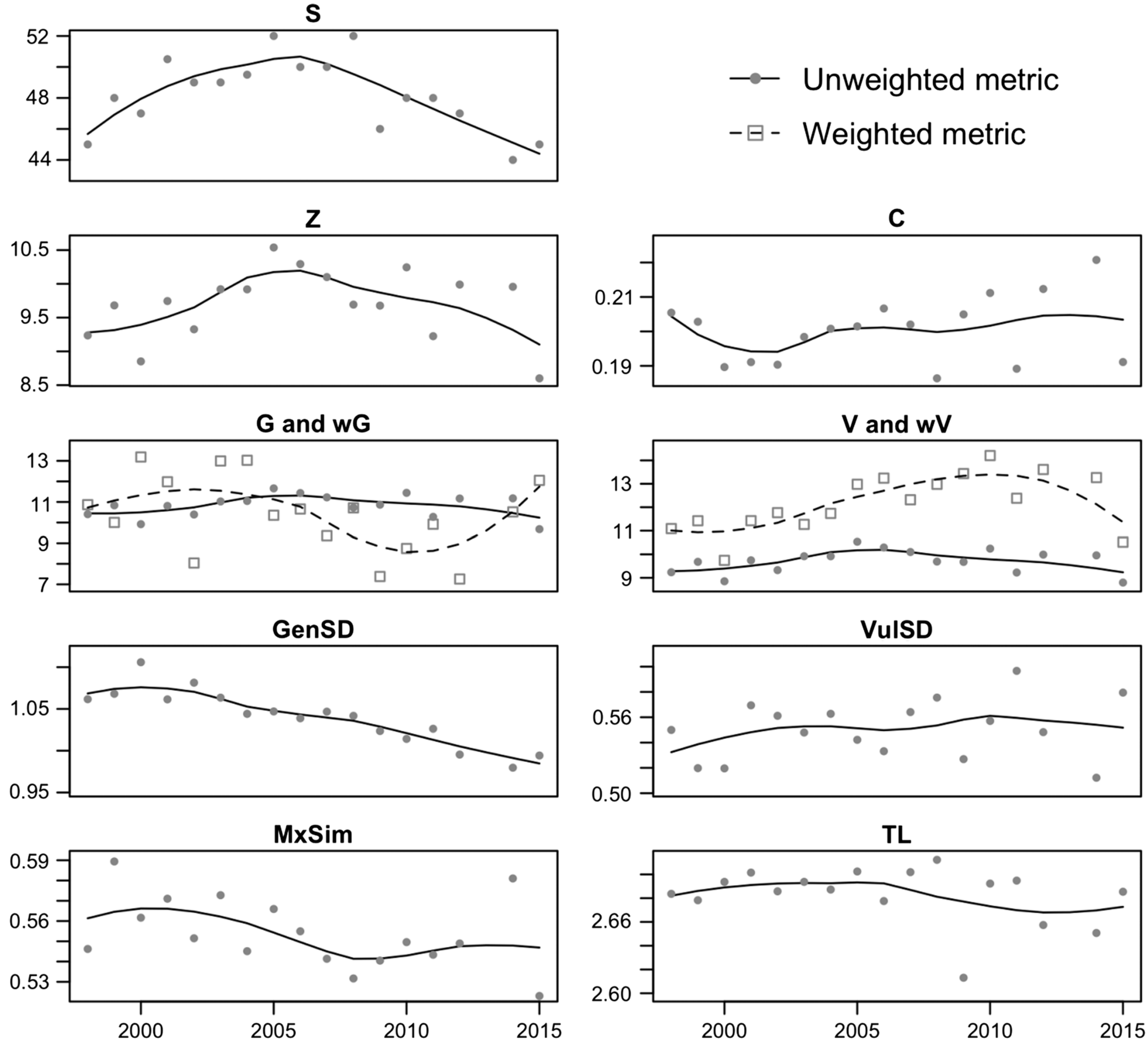

Figure 3. Time series of food web metrics. From left to right, top to bottom: species richness of the food web (S), link density (Z), connectance (C), generality with node-weighted generality (G and wG), vulnerability with node-weighted vulnerability (V and wV), normalized standard deviation in generality (GenSD), normalized standard deviation in vulnerability (VulSD), mean maximum trophic similarity (MxSim) and mean short-weighted trophic level (TL). The lines are the LOESS smoothing of the time series on the annual median bootstrap values (solid line with dots and dashed line with squares for unweighted and weighted metrics, respectively).

web snapshots subsampled from the metaweb are available in the appendix (Supplementary material Appendix 1 Fig. A5).

Temporal changes in food web structure

Food web structure varied over time following changes in the number of species. The species richness (S) of the food web increased from 45 to 52 species between 1998 and 2005, and then decreased to 45 species in 2015 (Fig. 3). Some metrics displayed changes related to this moderate peak in species richness: link density (Z), generality (G) and vulnerability (V) each showed a maximum around year 2005 (Fig. 3). The increase in link density shows that the species added to the food web during the first part of the time series were species with relatively many interactions. More specifically, this increase can be related to an increase in generalist predators or an increase in a predator's (realized) diet breadth. Connectance (C), on the other hand, decreased until 2000. After 2000, the trend reversed and the values gradually increased, but with markedly higher variability (Fig. 3). Overall, the values of the above-mentioned food web metrics in the early years were more similar to the values in the late years.

Other metrics showed diverging trends, or did not show much change over time at all (Fig. 3). Standard deviation of normalized generality (GenSD) gradually decreased over time, that is, the variation in the number of prey per predator decreased. Standard deviation of normalized vulnerability (VulSD), on the other hand, was always relatively low, with values < 1. The temporal changes in mean maximum trophic similarity (MxSim) were moderate, with a minimum in 2008. Mean short-weighted trophic level (TL) varied little over time and was, on average, relatively low (2.61–2.71). The temporal trends of the food web metrics were also confirmed using the three-year moving window (Supplementary material Appendix 1 Fig. A4).

Changes in food web structure relative to changes in community composition

The change in species richness shows that the species composition of the food web changed over time, albeit that we focus on the most persistent taxa. At peak species richness during 2005 (Fig. 3), almost all species in the metaweb were included in the annual webs and turnover was low (Fig. 4). After 2006, turnover of both species composition and interactions increased, with the turnover in species interactions being higher.

Assessing dissimilarity in food web species composition and interactions revealed that food webs at the beginning of the time series differed the most from food webs from the later years (Fig. 4), even though several food web metrics indicate equivalent trophic structure during these time periods (Fig. 3). Food webs with the highest dissimilarity differed more in terms of species interactions than in species composition (slope > 1, Fig. 4). During the time span of the study period, species with a high number of interactions, and more specifically a high number of prey, became more frequently present in the food web (Fig. 5). This was the case for a few flatfish species that were predominately absent in the early years of the time series (e.g. *Platichthys flesus*, *Scophthalmus rhombus* and *Hippoglossoides platessoides* with 28, 24 and 26 prey taxa, respectively).

Changes in food web structure relative to changes in species abundance

The local community changed, not only in species composition but also in dominance of taxa. Taxa that showed the largest increases in abundance over the time series, generally, had few prey but a high number of predators (no more than eight different prey taxa and up to 22 predators, e.g. planktivorous fish and the mollusc *Turritella communis*, Fig. 5). The brown shrimp *Crangon crangon*, on which many predators feed, showed a striking decrease in abundance, whereas *Crangon allmanni* greatly increased. In terms of numbers of prey and

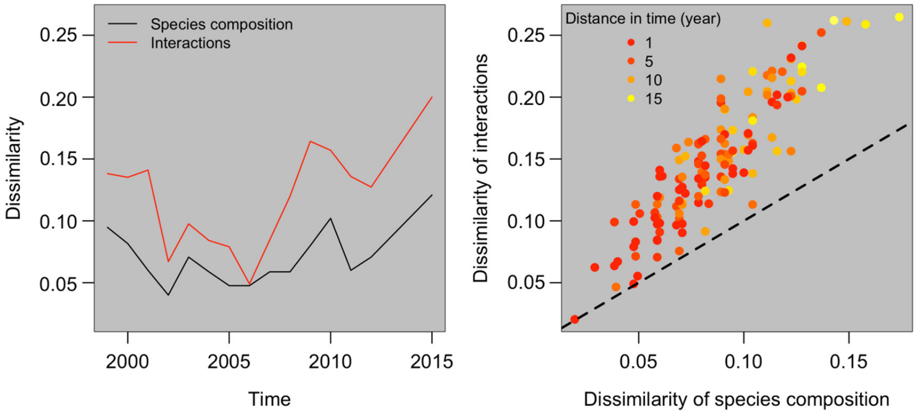

Figure 4. Dissimilarity of species composition and trophic interactions between food webs of consecutive years (left) and the relationship between dissimilarity of species composition and dissimilarity of trophic interactions for all pairs of food webs (right). The colour gradient indicates the time distance between food webs. The dashed black line indicates the 1:1 relationship.

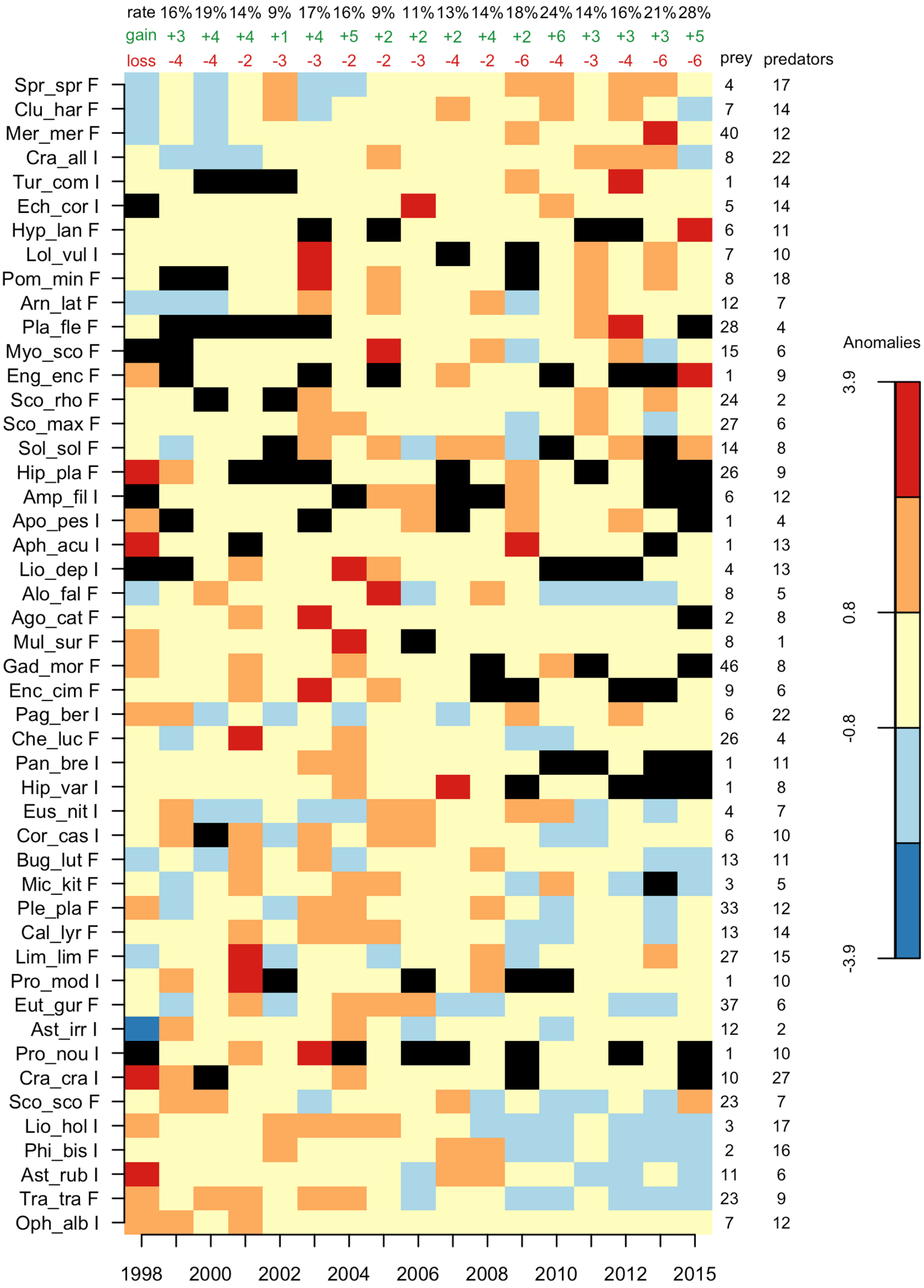

Figure 5. Time series of abundance anomalies. Red and blue colours indicate a difference between the median abundance of the year and the median over the time series. Black indicates a local extinction. Species are ranked by decreasing strength of their trend (approximated with the difference of their abundance in the first five years and the last five years) with the largest increase in abundance at the top and largest decrease in abundance at the bottom. The taxa names are abbreviated according to the species list, and a letter 'F' or 'I' indicates if the taxon is a fish or an invertebrate, respectively. At the top, green and red values give the number of species gained and lost from year to year. Values in black indicate overall percentage change in species composition, calculated as the sum of the number of species lost and species gained, divided by the number of species present in the previous year. On the right of the heatmap are indicated the number of prey and predators of each species.

predators, whiting *Merlangius merlangus* and the scaldfish *Arnoglossus laterna* stood out as exceptions among the species increasing in abundance (the former with 40 prey and 12 predators and the latter with 12 prey and seven predators). Additionally, some generalist predators – which were present at the beginning of the time series – decreased in abundance and were even absent from the food web during some years. For example, the Atlantic mackerel (*Scomber scombrus* with 23 prey) and Atlantic horse mackerel (*Trachurus trachurus* with 23 prey) showed some of the strongest negative trends, whereas cod (*Gadus morhua* with 46 prey) remained at low abundance throughout the time series.

The above-mentioned changes in species composition and dominance were reflected in the food web structure. Node-weighted generality (wG) was highly variable between years but decreased in the later part of the time series (dropping below unweighted values for generality, Fig. 3), revealing that more specialist taxa were abundant in the second half of the time series, whereas most generalist predators occurred at relatively low abundance after 2000. Node-weighted vulnerability (wV) was always higher than vulnerability and increased steadily to reach a maximum in 2010.

Discussion

In this study, we document how marine food web structure in an area within the German Bight varies over an 18-year time period (1998–2015). The German Bight food web underwent alterations in structural properties following changes in species richness, which first increased (1998–2005) and later decreased (2006–2015). During the first half of the time series, changes in food web structure were related to a shifting species composition of the community, in particular an addition of generalist benthivores (e.g. European flounder *Platichthys flesus* and brill *Scophthalmus rhombus*). For the second half of the time series, we found that changing food web properties likely mirrored the dominance of species in the community, with mainly planktivorous species, such as spat *Sprattus sprattus*, becoming more prevalent.

Temporal changes in food web structure

The observed increase in species richness between 1998 and 2005 mainly consisted of an addition of generalist benthivorous fish to the food web. Consequently, food web structure varied, showing changes in mean generality and vulnerability. Related to this, we detected asynchronous responses between species richness and complexity (i.e. connectance) of the food web. Numerous studies have argued that connectance co-varies inversely with species richness (e.g. reviewed in Dunne 2006). Based on this, we would expect connectance to decrease if the number of links increases linearly with the number of species (May 1972). For connectance to increase, however, there would have to be additions of 'new' taxa with a number of interactions higher than the link density in the previous year. Ecologically, this happens when the 'new' taxa are prey for many predators (i.e. increase predator diet breath), constitute predators for many taxa already present in the food web, or both – which is the case regarding the addition of generalist predators at intermediate trophic levels during the first half of the time series.

Several of the qualitative topology metrics (e.g. link density, generality) showed similar values at the beginning and at the end of the time series, although the underlying composition in species and trophic links was most dissimilar between early and late years. For example, with the local loss of species observed after 2005, the community contained a higher fraction of more specialized predators with generality decreasing to values observed before the peak in species richness. This suggests that although species composition and interactions change, qualitative food web structure can appear unchanged when comparing few time steps. For instance, Yletyinen et al. (2016) observed an increase in generality, but no significant changes in other structural properties, when comparing the structure of two Baltic Sea food webs for two different time periods; before and after a documented regime shift (late 1980s, Möllmann et al. 2009). Their limited number of time steps (i.e. two periods, 'before' and 'after') did not capture detailed temporal fluctuations in structural properties. It is possible that the Baltic Sea food webs transited from one state to another, but that food web structure at the network scale was maintained despite shifts in species composition. With a limited number of temporal snapshots (e.g. comparing two time periods 1998–2003 and 2010–2015), we would also not have been able to detect a temporal change in food web structure in the present study.

Changes related to composition in species and links versus changes in abundance

Node-weighted metrics revealed information complementary to that obtained from qualitative metrics. Qualitative topology metrics use species presence/absence data, and consequently, do not capture abundance changes in species populations. Our approach using node-weighted metrics to look at, for example, generality allowed us to detect changes in food web structure resulting from shifting dominance of species in the community. We identified instances where relative dominance of generalists, and later specialists, shifted node-weighted generality to deviate (with an increase, and a decrease, respectively) from the unweighted generality metric. The documented decline in benthivorous fish to the benefit of pelagic piscivores and planktivores goes in line with earlier observations for the time period 1973–2000 (Heath 2005) as well as the northerly migration of the horse mackerel *Trachurus trachurus* from the Southern North Sea (Reid et al. 2001). While it seems food web structure at the network level was similar between the early and late years of the time series, the baseline species composition and dominance of species differed. In particular, the recent community was more strongly dominated by specialists than what qualitative metrics could detect.

Node-weighted metrics can also display temporal variability matching that of their unweighted counterparts, although they may have higher or lower values overall (e.g. vulnerability before 2006). Similarity in the patterns between node-weighted and unweighted metrics reveals that changes in food web structure are primarily related to changes in species composition (from 1998 till 2006), whereas the subsequent difference in the patterns shows when changes in food web structure are more strongly related to changes in dominance of species (from 2006 till 2015). Similar behaviour between node-weighted metrics and their qualitative counterparts can suggest that, even if species composition changes, trophic interactions may be rebalanced through fluctuating abundances of species and changes in dominance of species (i.e. asynchronization of resources, McMeans et al. 2015). An empirical study focusing on temporal variability in terrestrial food webs showed temporal consistency in quantitative food web metrics, such as weighted generality, at the local scale during high compositional turnover (Kaartinen and Roslin 2012). They suggested that the stability of species composition may be partly resulting from a balancing between the abundance of species and their ecological specialization. High levels of turnover in species composition and trophic interactions coupled with a rebalancing in species abundances could be responsible for food web robustness and the rapid adaptability of the ecological community to change (Holling 1959). A constant reshuffling of species with varying ecological specialisation could allow for a progressive rewiring of the food web (Thierry et al. 2011). Further assessments of spatially and temporally resolved trophic interactions are needed to conclude on the restructuring mechanisms of food webs.

Ecosystem management: perspective, strength and limitations of our approach

Food web analysis is a powerful tool to summarize changes occurring at the ecosystem level. Yet, most ecological studies and management measures focus on single species, single trophic levels, or species of commercial interest and the species they interact with. However, studies that include a multitrophic approach are needed to make progress in ecology and to provide the necessary guidance for management (Seibold et al. 2018). For instance, the European Union requires moving towards a more ecosystem-based management through the Marine Strategy Framework Directive (MSFD 2008), which includes a specific descriptor for marine food webs (descriptor 4, Rogers et al. 2010). Numerous food web indicators, including structural indicators, have been proposed to evaluate Good Environmental Status (GES, Tam et al. 2017) but biomonitoring of food webs is still crucially lacking (Gray et al. 2014). Our methodology requires a metaweb and a way to assess changes in the community, taking advantage of available monitoring data. Combined with the right indicators, our analysis coupling topology and time series offers an easy-to-use and practical tool to monitor ecological changes at the community scale and to evaluate trends in the environmental status of ecosystems. However, our approach is highly dependent on the quality of the time series, making it challenging to draw any conclusions if the time series are too short or if the temporal resolution is too low. If high-quality data are available, and if an effort is put into building spatially and temporally resolved metawebs, our approach may become useful to reveal changes in the ecological status of ecosystems.

Currently, our metaweb displays values similar to older-generation food webs that have been criticized for overestimating structural food web properties (Dunne 2006). An overestimation of food web metrics is indeed pathological of cumulative food webs that are based on data on species' trophic interactions accumulated over larger temporal and spatial scales (Dunne 2006). Inferring trophic links (based on e.g. morphology) when feeding information is lacking (in our case accounting for 31% of interactions), is further likely to overestimate the number of links realized at any given time and influence food web properties. In addition, our food web does not consider the dynamics of the trophic interactions themselves and assumes that variability in trophic interactions only results from changes in species composition. This is obviously not true, and this assumption does not address consumer preferences and behaviours. Although our approach weights the presence of nodes and their links by the abundances of interacting species, it does not fully capture the dynamics of trophic interactions, as one cannot assume presence of interactions solely base on co-occurrence of species (Cazelles et al. 2016, Freilich et al. 2018). It is possible that some trophic interactions that we included are not temporally persistent or spatially dominant. Consumers may have different diets from year to year if they switch prey (e.g. ontogenetic diet shift) or if their preferred prey become more or less abundant (i.e. temporal coupling/decoupling, McMeans et al. 2015). Using stable isotopes, Silberberger et al. (2018) found that cod occupies the top position in the German Bight food web, whereas its position, in our metaweb, is lower and shared with other species. For cod, this is likely because the ontogenetic shift from predominant benthivory towards piscivory is not represented in our food web. Stable isotopes better mirror the larger reliance on larger and higher positioned prey known for larger cod individuals (Hislop et al. 1997).

Furthermore, it is likely that mobile organisms follow any periodicity in the availability of their preferred prey or in the physics of their environment. Timing becomes critical and consumers will locally occur when it is most favourable for them (e.g. match-mismatch between consumers and their prey, Durant et al. 2007). Variability in trophic interactions is believed to be responsible for the high adaptability of ecological communities and robustness of food webs in the face of change; and integrating spatial and temporal variability of trophic interactions will give better insight in the structure and functioning of food webs (Poisot et al. 2015, Ushio et al. 2018). We suggest that the integration of temporal variability in trophic interactions could be overcome by combining our approach with technics that estimate the probability of occurrence of trophic relationships (e.g. based on environmental and biological trait matching), which would allow for refining and improving both the metaweb and snapshots of food webs (Gravel et al. 2013, Morales-Castilla et al. 2015, Poisot et al. 2015, Bartomeus et al. 2016, Deyle et al. 2016). For instance, Albouy et al. (2014) projected the future structure of a marine food web under climate change with the help of environmental and biological trait data. In order to confirm our observations, such methodology could be coupled with a time series analysis of food web topologies to obtain more complete and better temporally resolved food web snapshots.

Concluding remarks

Food web structure varies through time, as we document with the marine food web of an area of investigation within the German Bight (North Sea). However, our study also shows that structural properties based on qualitative food web topology can have the same values between years despite different species composition and trophic interactions. In this study, we also weighted nodes by species abundances. Using these node-weighted metrics, we were able to detect changes in food web structure originating from shifts in dominance in the community. For the studied time series, we observed that food web structure was influenced by changes in species composition during the first half of the time series and more strongly by changes in species dominance during the second half. Although monitoring food webs through time remains challenging, our approach shows how using long-term ecosystem surveys can enable exploration of temporal variability in the structure of food webs.

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Author contributions – PO and RF contributed equally to this study. PO, RF and MCN conceived the original ideas and designed methodology with inputs from SK; PO, IK, HN and AFS collected the data; PO and RF analysed the data and prepared the figures; PO wrote the first draft of the manuscript. All authors contributed ideas for the interpretation of the data and the critical revision of the manuscript. All authors gave final approval for publication.

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Supplementary material (available online as Appendix ecog-04461 at <www.ecography.org/appendix/ecog-04461>). Appendix 1–2.