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Food web structure and community composition: a comparison across space and time in the North Sea

Romain Frelat, Susanne Kortsch, Ingrid Kröncke, Hermann Neumann, Marie C. Nordström, Pierre E. N. Olivier and Anne F. Sell

R. Frelat (https://orcid.org/0000-0002-8631-4398) ✉ (rom.frelat@gmail.com), Aquaculture and Fisheries Group, Wageningen Univ. and Research (WUR), Wageningen, the Netherlands. – S. Kortsch (https://orcid.org/0000-0002-6495-4781), M. C. Nordström (https://orcid.org/0000-0001-5763-1813) and P. E. N. Olivier (https://orcid.org/0000-0002-3755-3966), Environmental and Marine Biology, Åbo Akademi Univ., Turku, Finland. SK also at: Dept of Agricultural Sciences, Univ. of Helsinki, Helsinki, Finland. – I. Kröncke, Senckenberg am Meer, Dept for Marine Research, Wilhelmshaven, Germany and Inst. for Chemistry and Biology of the Marine Environment, Univ. of Oldenburg, Wilhelmshaven, Germany. – H. Neumann (https://orcid.org/0000-0001-9965-9443) and A. F. Sell (https://orcid.org/0000-0002-6556-7898), Thünen Inst. of Sea Fisheries, Bremerhaven, Germany.

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Ecological communities are constantly changing as a response to environmental and anthropogenic pressures. Yet, how changes in community composition influence the structure of food webs over time and space remains elusive. Using ecological network analysis, we assessed how food web structure changed across six distinct areas of the North Sea over a sixteen-year time-period. We used multivariate analyses to disentangle and compare spatio-temporal dynamics in community composition (i.e. changes in species abundances) and food web structure (i.e. changes in network properties). Specifically, we assessed how changes in community composition were reflected in food web structure. Our results revealed a strong spatial coupling between community composition and food web structure along a south–north gradient. However, the temporal covariation between community composition and food web structure depended on the spatial scale. We observed a temporal mismatch at regional scale, but a strong coupling at local scale. In particular, we found that community composition can be influenced by hydro-climatic events over large areas, with diverse effects manifesting in local food web structure. Our proposed methodological framework quantified and compared spatio-temporal changes in community composition and food web structure, providing key information to support effective management strategies aimed at conserving the structure and functioning of ecological communities in times of environmental change.

Keywords: community structure, ecological network analysis, food web, marine ecosystems, North Sea, spatio-temporal dynamics, tensor decomposition, trophic interactions

Introduction

Ecological communities are constantly changing as a response to environmental and anthropogenic pressures (Blowes et al. 2019). Understanding ecosystem dynamics is

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a prime focus of 1) community ecology, looking at changes in species diversity and community composition but ignoring feeding interactions; and 2) ecosystem ecology, looking at fluxes of matter or energy but ignoring species diversity (Thompson et al. 2012). Food web approaches provide an opportunity to bridge the gap between community ecology and ecosystem ecology by considering species diversity and the feeding interactions among them (Thompson et al. 2012, Gravel et al. 2019).

Food web ecology provides a framework to quantify how changes in community affect food web structure and its functioning (Baiser et al. 2019). There is a growing number of studies addressing how food web structure vary through either space (Pellissier et al. 2018, Braga et al. 2019, Kortsch et al. 2019, Gauzens et al. 2020) or time (Griffith et al. 2019, Olivier et al. 2019) but none of these empirical studies address the simultaneous changes in ecological communities through space and time. Recent modeling studies forecasted spatio–temporal changes in food web structure based on projected species distribution under climate change (Albouy et al. 2014, Hattab et al. 2016). Yet, these projections were derived from species distribution models that neglected trophic interactions. Therefore, empirical observations of abundance time series across multiple areas are needed to reveal how spatio–temporal changes in community composition influence food web structure.

Comparing the spatio–temporal dynamics of community composition and food web structure raises methodological challenges due to the high dimensionality and the complexity of the data. Here, we propose a comprehensive framework based on ecological network analysis and advanced multivariate analysis (Fig. 1). This framework relies on species abundance time series and a list of potential trophic interactions (i.e. a metaweb). First, we constructed snapshots of food webs over space and time from the metaweb and then computed multiple food web metrics to quantify food web structure. This methodology has previously been used to study food web dynamics over space (Havens 1992, Kortsch et al. 2019) and over time (Griffith et al. 2019, Olivier et al. 2019). Second, we used tensor decomposition (Leibovici 2010), a multivariate analysis to simultaneous investigate changes over space and time across multiple state variables (species abundances or food web metrics) (Frelat et al. 2017). Using tensor decomposition, we analyzed the spatio–temporal dynamics across multiple taxa (estimating community composition) and the subsequent changes in food web metrics (estimating food web structure) separately. Third, we compared the dynamics of community composition and food web structure. This comparison was performed at two spatial scales by comparing the temporal dynamics among and within locations, i.e. at regional and local scale, respectively. The three successive steps provide a comprehensive framework assessing how the spatio–temporal changes in community composition are reflected in food web structure.

To test our methodological framework, we used long-term abundance data from six different locations in the North Sea (Ehrich et al. 2007). The objective of this study is to understand how demersal fish and epifauna communities have varied over space and time by 1) identifying the dominant spatio–temporal dynamics in community composition and food web structure and by 2) comparing the dynamics between community composition and food web structure at regional and local scales.

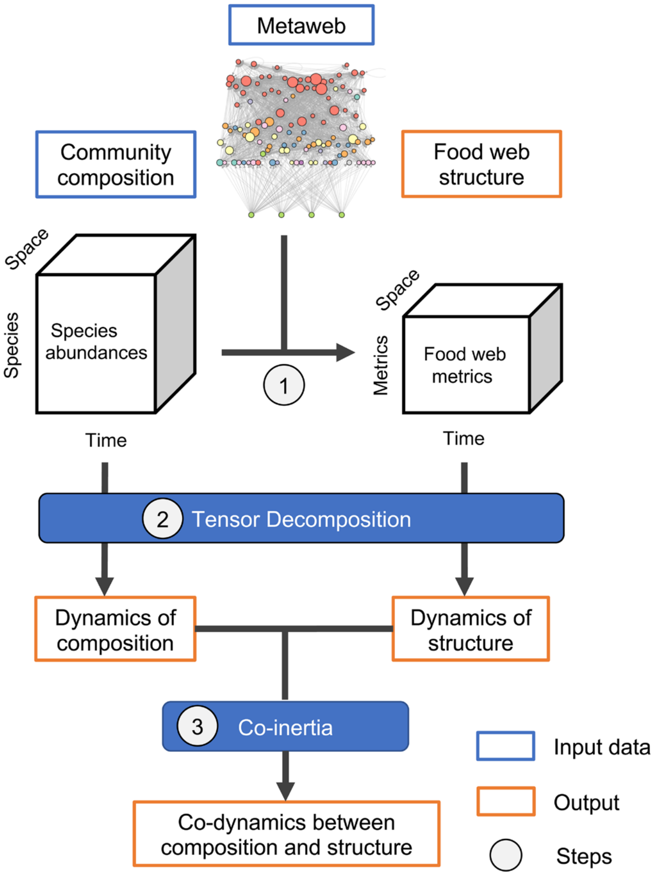

Figure 1. Schematic overview of the methodological framework. Using community composition (assessed by 114 species abundances) and a metaweb, the structure of food web snapshots in time and space are quantified by 16 metrics (step 1). Then, two tensor decompositions are calculated on community composition and food web structure separately to summarize their main spatio-temporal dynamics (step 2). Finally, co-inertia analysis is calculated to compare the dynamics of community composition and food web structure (step 3).

Material and methods

North Sea abundance dataset

Abundance data were collected during the German Small-scale Bottom Trawl Survey (GSBTS), a long-term, high-intensity scientific sampling in selected areas of 10 × 10 nautical miles (called boxes) spread across the North Sea (Ehrich et al. 2007). The survey monitors demersal fish in combination with benthic epifauna every summer since 1998. In each of the six boxes, demersal fish were sampled with an otter trawl at ~21 stations, and benthic epifauna with a 2-m beam trawl at ~9 stations. The positions of the six boxes were selected to cover a high diversity of habitats, including different combinations of hydrological and geographical conditions typical of characteristic subregions in the North Sea (Supporting information).

The GSBTS recorded 75 fish species and 369 epifauna species over the study period (1999–2014). We excluded pelagic fish species, and taxa that were only recorded occasionally, because their time series within the survey data may not represent their actual trends in the field. Thus, we only kept taxa that had been detected for at least nine years over the sixteen-year time period (Supporting information). In total, 43 demersal fish and 71 epifauna species were selected, accounting for 99% of the demersal fish abundances and 96% of epifauna abundances, respectively. The selected taxa comprised nine distinct taxonomic phyla. Chordata included fish taxa and the sea squirt *Ascidiella scabra*. Epifauna taxa mostly belonged to Arthropoda (n = 16), Cnidaria (n = 11), Echinodermata (n = 18) and Mollusca (n = 16). Eleven epifauna taxa occurred in colonies, for which the numbers of individuals could not be determined (e.g. Hydrozoa, Bryozoa and sponges). For these uncountable taxa, we recorded the occurrence of colonies, instead. The term 'community' refers to the studied demersal fish species and benthic epifauna together.

We calculated the relative species abundances by using Hellinger transformation on log transformed abundances (natural log(x + 1)). The Hellinger transformation is known to reduce the importance of species with high abundances (Legendre and Gallagher 2001). Additionally, using the relative abundances from Hellinger transformation facilitates the comparison of the abundances between species sampled by beam trawl (mostly epifauna) and species sampled by otter trawl (mostly fish). In the following text, 'abundance' refers to the Hellinger-transformed relative abundance and, thus, has no unit.

To eliminate possible bias due to differences in sampling effort among locations or years, we used a constant number of sampling stations (10 otter trawl stations and 5 beam trawl stations) over a two-year window. Because not all boxes were sampled every year by the intended number of stations due to extreme meteorological conditions or technical issues with the ship, we used a two-year sliding window that provides continuous and comparable time series of community composition at every location. Although the time-step is a two-year window, we refer to it in the following text as 'year', and every year cited in the text corresponds to a two-year window, e.g. 2001 refers to the period 2001–2002. We estimated the average abundance of each species per location and per time-step based on a random selection of the constant number of sampling stations. We repeated this random selection of stations 100 times, which provided 100 estimates of the spatio–temporal dynamics of species abundances. The analysis was repeated for each of these 100 abundance datasets. The scores from the tensor decompositions and co-inertia analysis presented below are the median score over these 100 repetitions.

Metaweb

A metaweb is a compilation of potential feeding interactions among all species found within a specific geographical area and time period, but does not represent observed realizations of trophic interactions at a given location and time (Dunne 2006). Subsampling trophic interactions from a metaweb based on community composition at a given location and time-step enables building multiple snapshot food webs across space and time that are methodologically consistent. Following the metaweb approach, co-occurring species with documented feeding links in the metaweb are assumed to interact across the geographical and temporal range, and consequently, changes in community composition beget changes in food web structure.

We compiled a metaweb containing the 114 taxa (fish and epifauna) and five aggregated trophic groups that were not sampled by the GSBTS survey but are important for food web structure: three primary producer groups (phytoplankton, benthic microalgae and macroalgae), one zooplankton and one detritus group (Supporting information). Detritus includes suspended organic matter, dissolved organic matter, organic particles such as marine snow and carrion. Information on the trophic interactions was collected through an extensive literature review of diet and feeding studies, expanding previous work for the southeastern box A (Olivier et al. 2019). We considered adult feeding links only and excluded feeding interactions involving juveniles, larvae or eggs. Despite a thorough review process, diet information for some taxa was still lacking. In this case, we inferred links, assuming that taxonomically closely related species (species within same genus or family) could share predators and prey. All inferred links were carefully double-checked using feeding ecology information and comparing size of prey and predators. Hence, our metaweb represents a network of potential trophic interactions between taxa. The species list and the metaweb with references are available as Supporting information.

Food web metrics

To describe changes in food web structure, we selected eleven unweighted food web metrics for each snapshot in space and time (Table 1, Supporting information). The calculation of unweighted metrics only considered species occurrences. Species richness (S), connectance (C), generality (G) and vulnerability (V) are classical properties capturing the main dimensions and horizontal structure of the food webs (Schoener 1989, Dunne et al. 2002). Short-weighted trophic level (TL) and the level of omnivory (Omni) describe the vertical trophic structure (Williams and Martinez 2004). Trophic coherence (Q) measures how neatly species fall into distinct trophic levels, a property influencing food web stability (Johnson et al. 2014). We assessed small-world properties, such as the mean shortest path between species pairs (Path) and the clustering coefficient (Clu), i.e. the probability that two taxa linked to a same third taxon are also linked together

Table 1. Description of the food web metrics. Abbreviations of metrics are shown in brackets. Metrics highlighted by a star indicate metrics also calculated with node-weighted averages, i.e. as weighted averages of node properties using nodes' relative abundances (Supporting information).

Metric	Definition	Ecological implications	References
Richness (S)	Number of taxa (nodes) in a food web	Taxonomic richness is an indicator of diversity	Schoener 1989
Connectance (C and wC)*	Proportion of all possible links that are realized (number of links divided by squared number of taxa)	A measure of network complexity that relates to the robustness of food webs in the face of perturbation	Dunne et al. 2002
Generality (G and wG)*	Average number of prey per predator	Indicates if the system contains more generalist or specialist species	Schoener 1989
Vulnerability (V and wV)*	Average number of predators per prey	Indicates the degree to which species function as prey	Schoener 1989
Trophic level (TL and wTL)*	Average of the short-weighted trophic level, calculated for each node as the mean of the prey-average trophic level and the shortest trophic level	A measure of how many steps energy must take to get from an energy source to a focal taxon	Williams and Martinez 2004
Omnivory (Omni and wOmni)*	Average standard deviation of TL of prey per predators	Average level of diet width, which is known to influence stability	Williams and Martinez 2004
Incoherence (Q)	Incoherence is the standard deviation of the trophic distance of all links in the food web	Trophic coherence is associated to food-web stability	Johnson et al. 2014
Path Length (Path)	Characteristic path length is the mean shortest path between two taxa	A simple measure of how quickly effects can spread throughout a food web (Dunne et al. 2013)	Watts and Strogatz 1998
Clustering (Clu)	The clustering coefficient describes the probability that two taxa that are linked to the same taxon are also linked together	Food webs with higher clustering contain taxa that are more highly interlinked	Watts and Strogatz 1998
Modularity (Mod)	Modularity describes how densely sub-groups of species interact with one another compared to species from other sub-groups	Indicates the presence of densely linked sub-groups within a network, which could prevent the spread of perturbations	Guimerà and Nunes Amaral 2005
Maximum trophic similarity (Sim)	Mean of all species largest diet similarity	Reflects the level of niche overlap and competition for food	Williams and Martinez 2000

(Watts and Strogatz 1998). Modularity (Mod) quantifies the extent to which sub-groups of species (called modules) interact more within than between sub-groups (Guimerà and Nunes Amaral 2005). The presence of densely linked modules could prevent the spread of perturbations (Landi et al. 2018). To find the best partition, we used the simulated annealing algorithm (Reichardt and Bornholdt 2006), a stochastic optimization approach that identifies modules by maximizing the modularity function (Newman and Girvan 2004) implemented in the function '*cluster_spinglass*' in the R package 'igraph' (Csárdi and Nepusz 2006). Niche overlap was evaluated as the average maximum diet similarity (Sim) (Williams and Martinez 2000).

In addition to the unweighted metrics, we calculated five node-weighted metrics (Supporting information). Node-weighted metrics capture changes in species abundances, assuming that dominant species have a strong structuring role in the food web (Olivier et al. 2019, Kortsch et al. 2021). These metrics are weighted averages of node properties using nodes' relative abundances. For instance, node-weighted generality is calculated as the average number of prey per predator, weighted by the relative abundance of the predator.

In total, we calculated sixteen network metrics on the temporally and spatially resolved food web snapshots. For each location and time-step, a list of the species was compiled and used to subsample trophic interactions from the metaweb. To compute the node-weighted metrics, we used the relative abundances estimated from the Hellinger transformation. For the five trophic groups and eleven epifauna taxa with no estimates of abundance, we assigned, when present, a constant abundance corresponding to the average relative abundance of all other species. Because these values are constant, this approximation on the five trophic groups has no effect on the relative dynamics of node-weighted metrics. For the eleven uncountable epifauna taxa, using average abundance provide them with a similar weight as most taxa, without overweighting nor downweighing these taxa compare to the community. In a sensitivity test, we found similar dynamics and results when these taxa were discarded for the calculation of node-weighted metrics (Supporting information).

Tensor decomposition

Tensor decomposition allows the simultaneous investigation of changes over space and time across multiple state variables. Inherently, spatio-temporal datasets consist of three dimensions: 1) the state variables measured (in our case, species abundances or food web metrics), 2) the location of the measurement and 3) the time of the measurement. Tensor decomposition is an extension of a 2-dimensional multivariate analysis such as principal component analysis (Cichocki et al. 2015). The objective is to summarize the maximum variability of the original dataset in a minimum number of components while considering the covariations between these three dimensions. Among tensor decomposition methods, principal tensor analysis (PTA) is a generalization of singular value decomposition and offers an easy-to-interpret and robust method to decompose a tensor (Leibovici and Sabatier 1998, Frelat et al. 2017). We performed two PTAs to separately investigate the spatio-temporal dynamics of 1) community composition and 2) food web structure (Fig. 1, step 2). We scaled the two sets of variables (abundance per species and food web metrics) so that their specific average values across the locations and time series equaled zero and their standard deviation equaled one. The scaling removed the differences in units for food web metrics, and the differences in dominance between species, focusing the analysis on species-specific abundance anomalies. Therefore, the tensor decomposition of community abundances is calculated on the anomalies of Hellinger transformed abundances.

The percentage of variance explained by each successive principal tensor (PT) indicates the number of significant PTs, i.e. the best trade-off between the minimum number of PTs and the maximum percentage of variance explained (Cattell 1966) (Supporting information). PTs provide scores for the three dimensions: species or food web metrics, location and time. Each PT was interpreted based on its temporal and spatial scores, plotted in a 2D heatmap that represented the dominant spatio-temporal dynamics in the dataset. The interpretation of PTs is similar to the interpretation of principal components in PCA. Scores with high absolute values are the most meaningful while the scores close to 0 are not well captured by PTs. The high number of species (n = 114) rendered the interpretation of the species' scores difficult. Hence, we computed Euclidean distances between species based on their scores on the PTs and subsequently conducted a hierarchical cluster analysis based on Ward's criterion (Ward 1963). We selected the number of groups from a graphical interpretation of the dendrogram (Supporting information). The clustering provides a simplification of the dynamics of the multitude of species into fewer sub-assemblages, sharing similar spatio-temporal patterns. The clusters were named using the letter of the Box, in which organisms from the respective cluster had the highest average abundance. We added a sign ('+' for increasing or '−' for decreasing) when the clusters showed strong temporal dynamics.

Comparison between community composition and food web structure

The two tensor decompositions were compared using a co-inertia analysis highlighting the spatio–temporal co-dynamics between community composition (i.e. species abundances) and food web structure (i.e. measured by food web metrics) (Dray et al. 2003) (Fig. 1, step 3). Co-inertia is an unconstrained symmetric analysis searching for axes that maximize the covariance between two tables. Here, we applied co-inertia analysis on the results (i.e. scores) of the two tensor decompositions. The 3D tensors were transformed into 2D matrices with time and space collated into a single dimension, consisting of the unique combinations of years and locations. Co-inertia analysis identifies principal components (PCs) representing the spatio–temporal dynamics with highest covariance between community composition and food web structure among Boxes, later referred to as regional co-dynamics. By comparing the scores of species and food web metrics on these PCs, we can identify which species and which network properties were associated with the dominant co-dynamics.

Additionally, we investigated the within-location temporal relationship between community composition and food web metrics. For each location, we calculated a separate co-inertia analysis to explore the local co-dynamics. We then compared the six local co-dynamics to assess whether the identified co-dynamics were synchronous among boxes and whether the relationship between food web metrics and community composition was similar across the North Sea. Therefore, we conducted two hierarchical clustering analyses to evaluate the degree of similarity among the co-dynamics. The first clustering compared the temporal scores on PC1, grouping synchronous co-dynamics. The second clustering compared the food web metrics scores on PC1, grouping similar structural changes in the food web. Furthermore, we tested the association between the dynamics of community composition and food web structure with a Monte–Carlo permutation test and the RV coefficient (Heo and Gabriel 1998). The RV coefficient is a generalization of Pearson's correlation coefficient for matrices (instead of vectors). The permutation test with 1000 random permutations was performed for each box separately to evaluate whether the association between the temporal dynamics of community composition and food web structure was significantly stronger than expected by chance.

Software

All statistical analyses were conducted in the programming environment R ver, 4.0.2 (<www.r-project.org>). Food web analyses were conducted with the package igraph ver. 1.2.5 (Csárdi and Nepusz 2006), the tensor decomposition was calculated with the package PTAk ver. 1.3 (Leibovici 2010) and the co-inertia analysis with the package ade4 ver. 1.7 (Dray and Dufour 2007).

Results

Dynamics of community composition

The dynamics of community composition were summarized by five principal tensors (PT) explaining in total 57% of the variability (Fig. 2, Supporting information). The first three principal tensors (PT1–3) highlighted differences among locations but not among years as shown by homogeneous horizontal lines in the heatmaps, indicating strong spatial structuring of community composition (Fig. 2a). PT1 highlighted the south–north gradient in the North Sea, and specifically, the difference in community composition between the southernmost box (A), with highly negative score, and

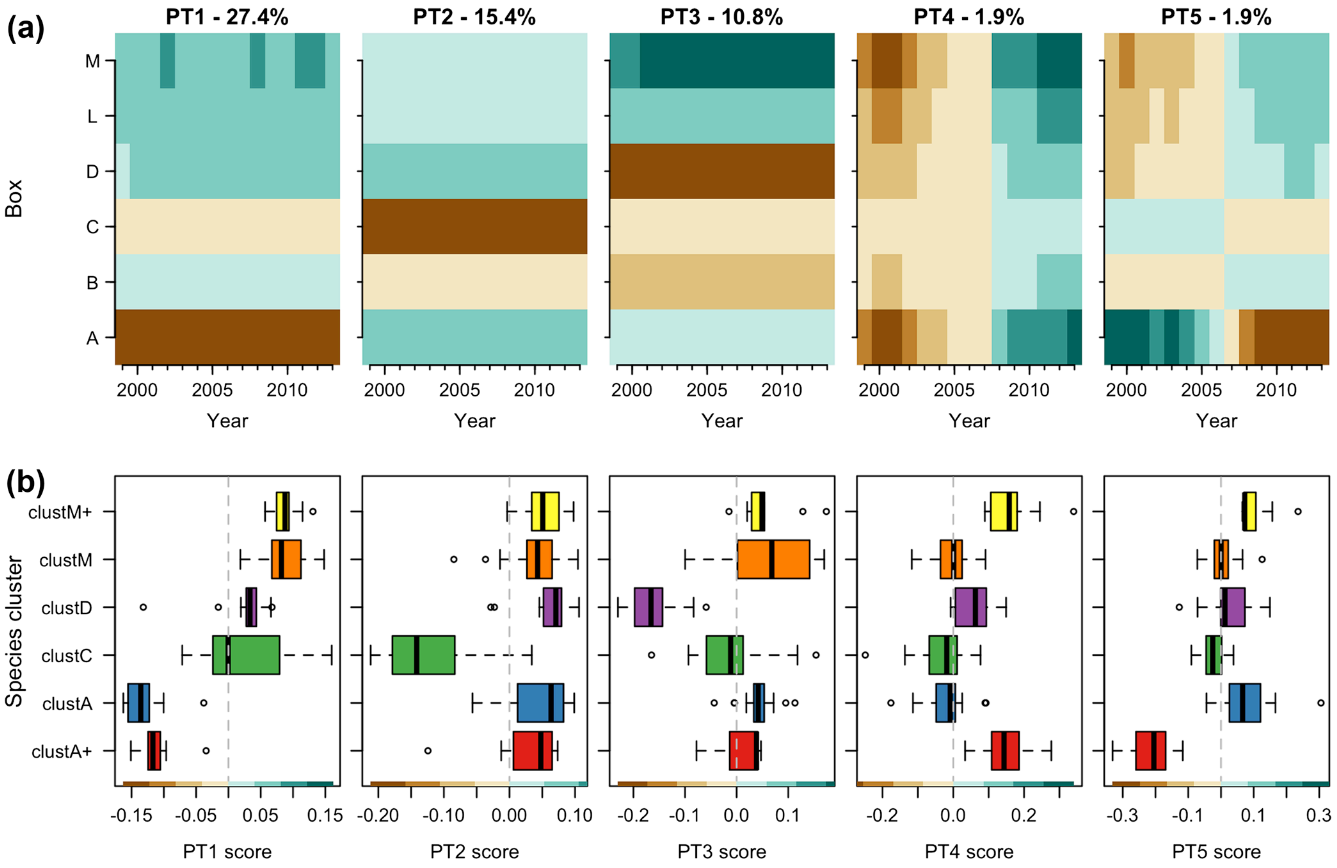

Figure 2. Tensor decomposition of community composition. The PTA revealed five Principal Tensors (PT) with (a) spatio-temporal scores represented as heatmaps with time on the x-axis and locations on the y-axis and (b) species scores grouped in 6 different clusters of species. Four clusters were characterized solely by their spatial distribution (with the letter referring to Box with highest abundance: clust A, C, D and M) and two clusters showed an increasing temporal trend: in Box A (clustA+) and in Box M (clustM+). The percentages shown are the additional percentages of variance explained by the successive PTs. The color scale goes from brown for highly negative score to dark green for highly positive scores.

the northernmost box (M), with highly positive score. PT2 revealed a unique community composition in box C, with highly negative score compared to other boxes that have relatively low absolute scores. The east–west gradient was reflected in PT3 with negative scores for boxes in the northwest (B and D) and positive scores for boxes in the northeast (L and M).

The last two principal tensors (PT4–5) summarized the temporal dynamics of the communities, as shown by the heterogeneous horizontal lines in the heatmaps (Fig. 2a). PT4 showed a common trend among all boxes with low values in 1999–2002 and highest values in 2009–2015. This trend was particularly strong in the southernmost (A) and northernmost (L and M) boxes. PT5 highlighted an opposite temporal trend in box A versus boxes L and M. PT4–5 changed signs around 2006–2008, which suggests a major reorganization in community composition during this period.

To summarize the dynamics of the multitude of species (n = 114), we conducted a cluster analysis on species' scores and grouped the species into six clusters. These clusters consist of species that share similar spatio-temporal dynamics (Fig. 2b, Supporting information). Four clusters had no or weak temporal dynamics and were characterized by their spatial distribution (clust A, C, D and M). For instance, clustA grouped 21 species that are predominantly occurring in box A, such as the flatfish *Solea solea* or the sea snail *Euspira nitida*. Similarly, clustC grouped 34 species caught in majority in box C, clustD consisted of 13 species distributed preponderantly in box D, and clustM grouped 30 species mostly found in box M. Both vertebrate (Chordata, i.e. mostly finfish and elasmobranchs) and invertebrate taxa (Arthropoda, and Mollusca) were found in these four groups (Supporting information). ClustA, the group of species predominantly in box A, was different from the other clusters because of the large proportion of fish (Chordata) and the absence of Cnidaria (e.g. sea anemones and hydrozoans). Additionally, two clusters showed a strong increasing temporal trend, in box A (clustA+, 7 species) or in box M (clustM+, 9 species). Hence, the clustering analysis confirmed that species with the strongest temporal dynamics are found in boxes A and M (Supporting information). In box A, species with increasing abundance included Chordata (e.g. the flatfish *Platichthys flesus*), Mollusca (e.g. the bivalve *Chamelea gallina*) and Echinodermata (e.g. the sea urchin *Echinocardium* *cordatum*). In box M, species that increased their abundance are Arthropoda (e.g. the crab *Inachus dorsettensis*), Chordata (e.g. the finfish *Merluccius merluccius*) and Cnidaria (the hydroid *Hydrallmania falcata*) (Supporting information).

Dynamics of food web structure

The spatio-temporal dynamics of food web structure were summarized by four PTs explaining 63% of the variability of the sixteen food web metrics (Fig. 3). PT1–3 revealed strong spatial differences among boxes. PT1 highlighted the difference between the food webs in box A and box M with, in box A, higher connectance (C and wC), higher omnivory (Omni, wOmni) and higher clustering (Clu) but lower richness (S), lower vulnerability (V and wV) and lower generality (G, wG). In other words, communities in the southern North Sea contain fewer species, with a lower diversity of prey and predators, and that are densely connected compared to communities in the northern North Sea.

PT2 revealed that food web structure in box B differed from food web structure in box D because of higher diet overlap (Sim), and lower average trophic level (TL) and vulnerability (V) (Fig. 3). Hence, the community in box B had fewer top predators, shorter food chains and more overlap in diets compared to the community in box D. PT3 highlighted the unique structure of the food web in box C, with high modularity (Mod), high average shortest path (Path) and a low clustering coefficient (Clu). Thus, the food web in box C had strongly divided modules with low connectivity between them.

PT4 was the only PT showing strong temporal dynamics especially in the food webs of boxes A and M. In 1999–2002, the food webs had lower diversity of prey (G, wG) and predators (V), and lower shortest path lengths between taxa, compared to the period 2006–2007. The dynamics were opposite and weaker in boxes B and D.

Co-dynamics between community composition and food web structure

The co-inertia analysis, comparing the spatio-temporal dynamics of community composition (i.e. species abundances) and food web structure (measured by network metrics), identified two main axes of covariation across the North Sea (Fig. 4). As expected from the two separate tensor decomposition results, the strong south–north gradient in the North Sea was identified as the strongest axis of covariation, explaining 85% of the covariance. The community

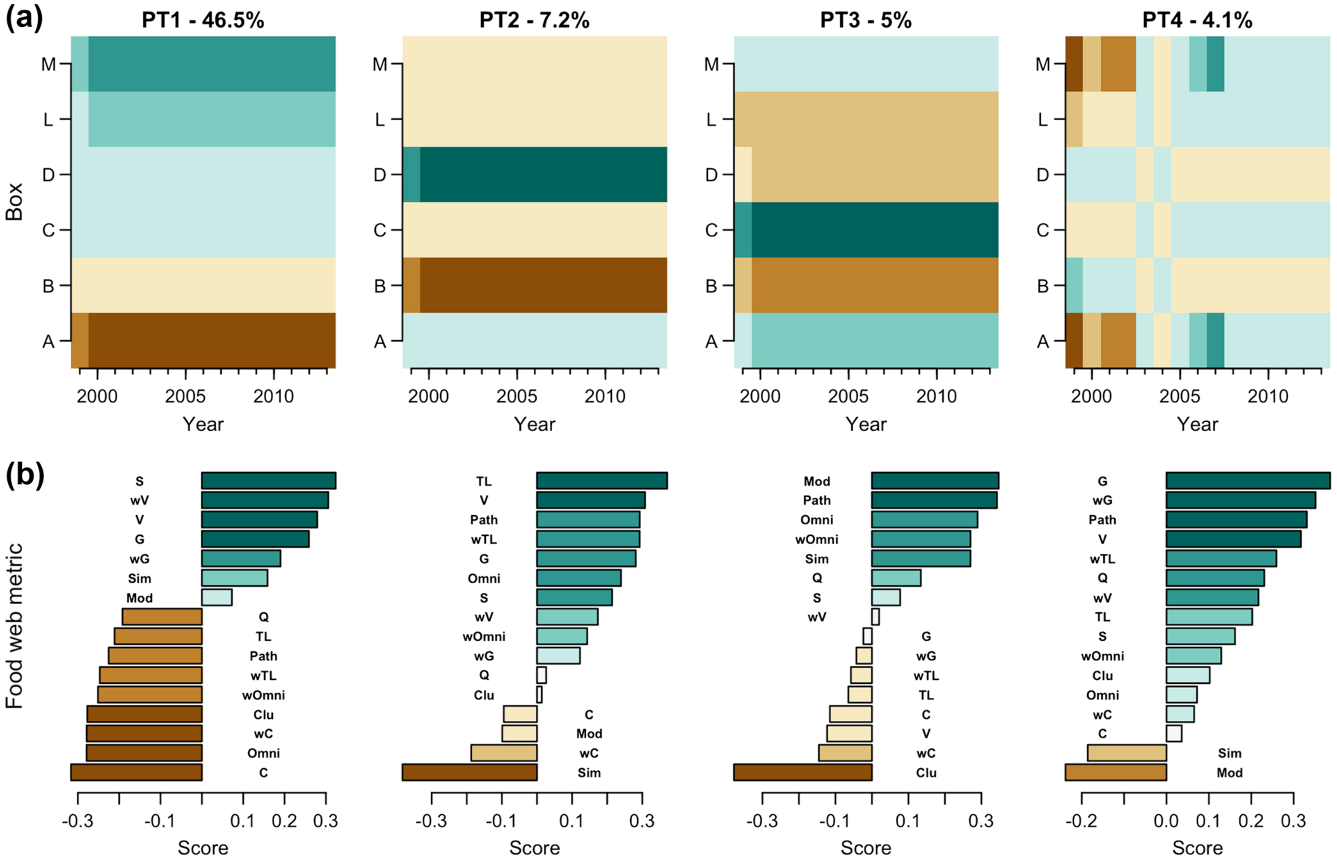

Figure 3. Tensor decomposition of food web structure. The PTA revealed four Principal Tensors with (a) the spatio-temporal scores represented as heatmap with time on the x-axis and location on the y-axis. (b) The scores of the food web metrics are shown as horizontal bars in increasing order. The abbreviations of the metrics are explained in Table 1. The percentages shown are the additional percentages of variance explained by the successive PTs. The color scale goes from brown for highly negative score to dark green for highly positive scores.

in box A had fewer species, mainly limited to species from clustA and clustA+, but higher connectance (C and wC) and omnivory (Omni and wOmni) compared to box M. On the contrary, box M was composed of numerous species from clustM, clustM+ and clustC, and the food web had higher richness (S) with many prey and predators per taxa, resulting in high vulnerability (V and wV) and generality (G and wG). However, these species were on average less omnivorous (Omni and wOmni), leading to a lower density of interactions (estimated as connectivity, C and wC).

Another source of covariation between community composition and food web structure is the difference between boxes C and D, which explained an additional 6.7% of the covariance (PC2, Fig. 4). PC2 highlighted differences in community composition with opposite scores for species in clustC and clustD. Compared to box D, food web structure in box C had higher modularity (Mod), higher diet overlap (Sim) but lower average trophic level (TL and wTL).

At the regional scale of the North Sea, the co-inertia analysis revealed an absence of temporal covariation between community composition and food web structure. This temporal mismatch was partly observed when comparing the temporal scores from previous separate tensor decomposition on community composition (PT4–5) and food web structure (PT4) (Supporting information).

Local temporal co-dynamics

The temporal co-dynamics between community composition and food web structure were further explored by within-location co-inertia analysis. At the local scale, Monte-Carlo permutation tests showed that temporal dynamics of community composition were strongly and significantly correlated with food web structure for all boxes (p-values < 0.01) except for box D (p-value = 0.04) (Supporting information). Nevertheless, the identified local co-dynamics differed among Boxes (Fig. 5). Two separate hierarchical clustering analyses on temporal scores and food web metrics scores coherently revealed three pairs of geographically neighboring Boxes with distinct temporal co-dynamics.

In boxes A and C (southeastern North Sea), an abrupt change occurring between 2007 and 2008 separated two distinct periods, as indicated by the relatively low score in 2000–2007 followed by highly positive scores in the years 2008–2013 (Fig. 5a, Supporting information). The highly positive scores of generality and vulnerability and the highly negative scores of modularity and trophic level (Fig. 5b) indicated that, during the early period (1999–2004), food web structure had lower generality and vulnerability and higher modularity and trophic level compared to the most recent period (2008–2013) (Fig. 5b). Interestingly, these similar and simultaneous changes were driven by different species in the two boxes (Supporting information). In box A, the most recent period is associated with an increase in species from clustA+, whereas the community in box C was mostly affected by changes in abundance of species from clustC (Supporting information).

In boxes L and M (northern North Sea), the linear trends in temporal scores (Fig. 5a, Supporting information) suggest a gradual change in species composition associated with a linear increase in food web richness, vulnerability, generality and maximum shortest path, and a decrease in omnivory and connectance (Fig. 5b). The species that contributed the most to these changes are species from clustM+ (Supporting information). In boxes B and D (western North Sea), the period 2006–2008 was different in terms of community composition as well as in terms of food web structure with lower richness, lower modularity, higher connectance and higher clustering coefficient compare to the rest of the time series (Fig. 5).

Discussion

This study identified and disentangled dominant spatio–temporal dynamics and relationships between species community composition and food web structure. We identified a strong coupling in space with community composition and food web structure following a south–north spatial gradient. Curiously, temporal co-variation between community composition and food web structure depended on the spatial scale. We found a temporal mismatch at the regional scale, i.e. no simultaneous co-dynamics among boxes across the North Sea, but a strong coupling at the local scale, indicating that local changes in species composition had different impact on the food web structure. These empirical results contribute to the ongoing discussion about how ecological networks are structured over space and time (Poisot et al. 2015, Tylianakis and Morris 2017, Baiser et al. 2019).

Large-scale dynamics

The spatial patterns in community composition and in food web structure mirror the strong environmental gradient along the south–north axis in the North Sea. This well documented latitudinal gradient in North Sea community composition has been linked to hydrographic variables such as bottom water temperature (Callaway et al. 2002). The 50-m depth contour in the North Sea has been identified as a conspicuous boundary, separating fish and epifauna communities, because it closely matches the edge between mixed and stratified waters (Ehrich et al. 2009, Reiss et al. 2010). The northern epifauna community is more diverse than its southern counterpart, partly driven by the absence of sessile species in mixed waters at shallow depth in the South while being highly abundant at deeper locations with stratified water in the North (Neumann et al. 2008b). This spatial difference was also observed in the clustering of species dynamics, with the absence of the phylum Cnidaria and the large proportion of fish among species spatially distributed in southern box A. Additionally, our results revealed distinct food web structures linked to latitudinal differences in community composition. The diverse epifauna in the northern boxes (L and M) led to food webs with higher richness, but lower density of

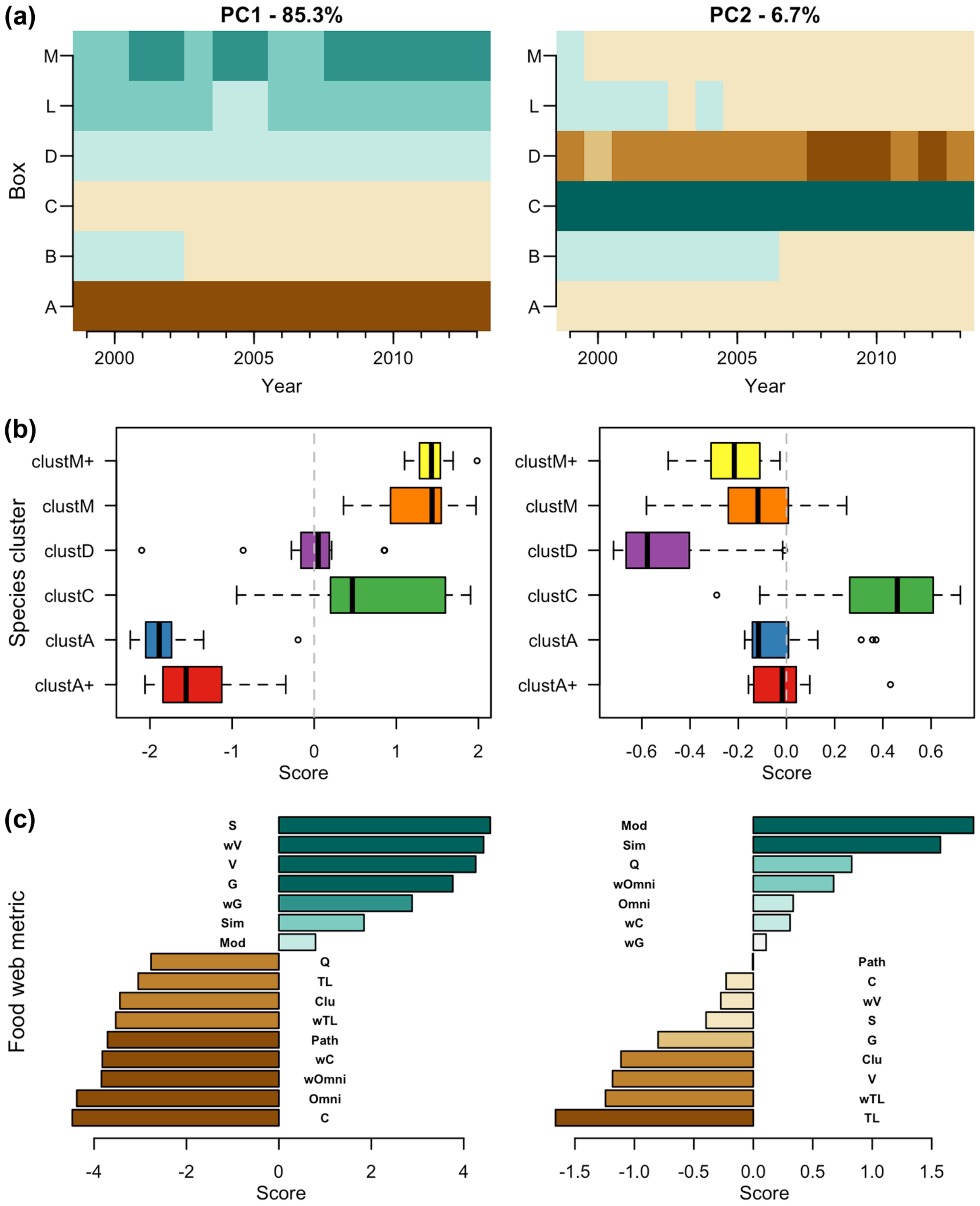

Figure 4. Co-inertia analysis between community composition and food web structure. The two principal components of covariance are represented with (a) spatial and temporal scores as heatmap with time on the x-axis and location on the y-axis, (b) species scores grouped by clusters, and (c) food web metric scores. The abbreviations of the metrics are explained in Table 1. The percentages shown are the additional percentages of covariance explained by the successive PCs. The color scale goes from brown for highly negative score to dark green for highly positive scores.

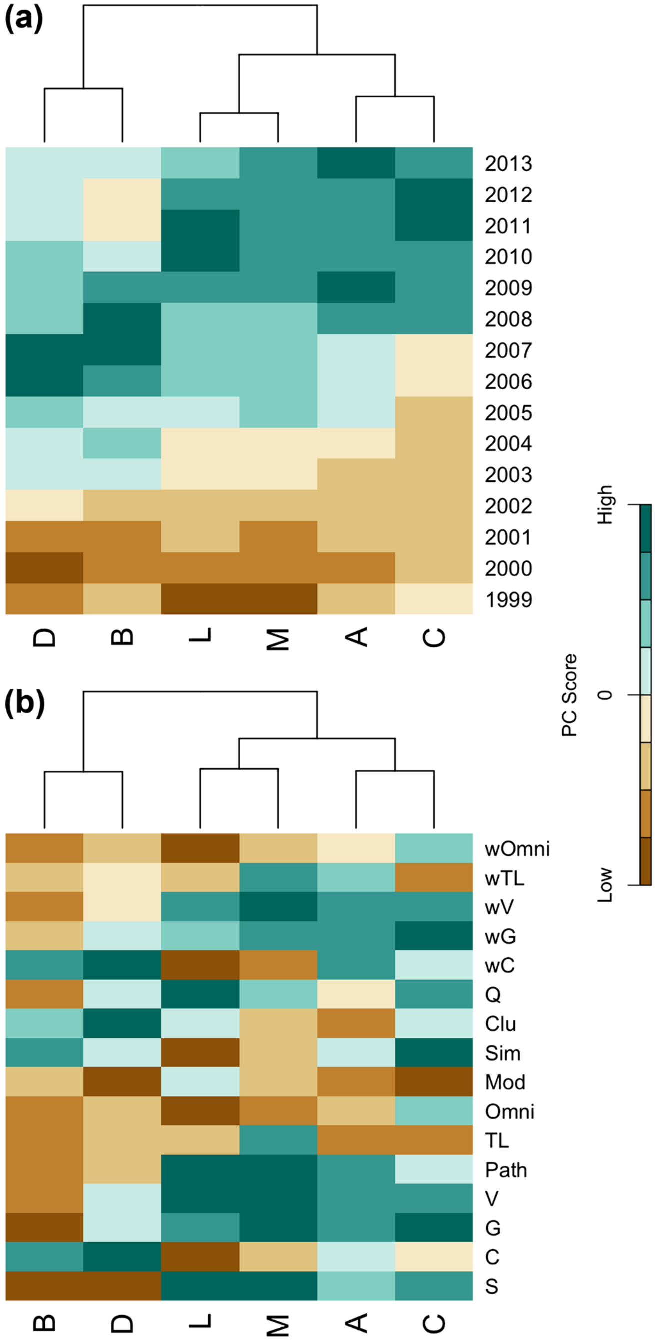

Figure 5. Within-location temporal co-dynamics between community composition and food web structure. The scores of (a) years and (b) food web metrics on the first principal component of the within-Box co-inertia analyses are represented for the 6 Boxes (in x-axis). The abbreviations of the metrics are explained in Table 1.

connections among species. On the contrary, the large proportion of omnivorous fish and the less diverse epifauna in the southern box A was related to a smaller but denser food web.

In a latitudinal comparison of food web structure in terrestrial vertebrate assemblages, two major axes of variability were identified, namely one related to species richness and mean trophic level, and a second related to the connectance and proximity of species within the web (Braga et al. 2019). While our results confirm that species richness is one of the main changes in food web structure (i.e. with high scores in the first axis), we found that connectance was negatively associated to changes in richness and that trophic level was associated with a separate component, indicating a disconnect between changes in richness and changes in trophic levels. Such differences suggest that the processes behind food web structure dynamics may be context-dependent. In our results, changes in species richness explained most of the covariance in the regional co-dynamics (i.e. north–south gradient). Yet, at the local scale, temporal changes in species richness were not always associated with corresponding changes in food web structure. For instance, higher species richness was associated with an increase in average shortest path but a decrease in omnivory in boxes L and M, whereas it was associated with an increase in modularity and a decrease in clustering coefficient in boxes B and D. Additionally, the temporal dynamics in boxes A and C were not associated with changes in species richness, demonstrating that food web structure can change while species richness remains relatively constant. Together, these results highlight the need to account for species interactions to more fully understand changes in ecological community structure.

A common temporal trend was identified in community composition, particularly strong in box A and M and with rapid changes in 2006–2008 (Fig. 2). This shift was caused by the increase in abundances of different fish and epifauna taxa, grouped into two distinct clusters clustA+ and clustM+ for box A and M, respectively. This period of drastic change coincided with quasi-synchronous biological shifts in phytoplankton, benthic epifauna and temperate reef fish in different marine ecosystem worldwide (Pacific, Arctic, Baltic-, North- and Mediterranean Sea) (Kröncke et al. 2019). These shifts were related to large-scale hydro-climatic forcing namely the position of the Icelandic low, which determines the flow of the Gulf stream. Interestingly, at the regional scale, food web structure did not follow the same temporal dynamics than community composition. These findings suggest that community composition can be influenced by hydro-climatic events over large spatial scales, but with different impact on the food web structure at the local scale.

Local temporal dynamics

The within-location temporal analyses revealed synchronous dynamics between community composition and food web structure at the local scale. Our results highlighted three different pairs of neighboring Boxes exhibiting similar dynamics, influenced by different water masses (Ehrich et al. 2009). For instance, epifaunal communities in the southern North Sea are more affected by climate-induced temperature increase than northern epifaunal communities (Neumann et al. 2008a, 2009). Two different currents strongly influence the composition and the dynamics of epifauna communities in the northern North Sea (Schückel et al. 2010). In the northwest, the vertically mixed water column and the major flow of Atlantic current (Fair Isle current) results in increasing SST and a deeper light penetration, which enhances primary production and food supply. In the northeast, the water column is stratified and increasing temperatures strengthen this stratification resulting in decreased in food availability. Together these results indicate that spatial differences in local water masses can lead to different food web dynamics. This has implications for marine management design, and highlights the need to separate the North Sea in to at least three distinct management areas: southern (boxes A and C), northwestern (boxes B and D) and northeastern (boxes L and M).

Curiously, boxes A and C show synchronous dynamics in food web structure despite hosting completely different communities (respectively dominated by clustA and clustC). The strong shift in 2007–2008 affected different species but resulted in comparable changes in food web structure, with decreased average trophic levels and modularity as well as increased vulnerability and generality (Fig. 5). Our results suggest that large-scale climatic forcing, or other anthropogenic pressures, might have affected different species but with similar topological role (or trophic position) in the food web. Unfortunately, it is hard to distinguish a causal relationship, and our framework cannot determine whether changes in community composition are due to selection of species' traits or selection based on the species' roles in the network (Dormann et al. 2017).

A framework to study food web dynamics

Our methodological framework captures only changes in food web directly linked to changes in species abundance. It does not consider other sources of structural changes, such as changes in interaction strength or changes in co-evolutionary processes (Tylianakis and Morris 2017, Bartley et al. 2019), because such data are scarce and only available for a handful of well-studied species. Using a metaweb constrains the amount of variation in the food web and may thereby inadequately capture the link between community composition and food web structure. However, despite using such a simplified framework, our results indicate that changes in community composition were not always triggering changes in food web structure. Similar results were reported beyond the North Sea. For instance, in the Baltic Sea and the Barents Sea, motifs configurations (i.e. tri-trophic submodule) were conserved despite major documented changes observed in community composition (Yletyinen et al. 2016, Griffith et al. 2019). Additionally, our results show that the coupling between changes in community composition and food web structure is complex and depends on the spatial scale. Therefore, the impacts of future changes in community composition on the ecosystem structure will be hard to predict without considering the network of trophic interactions. For instance, we found that large-scale hydro-climatic events might modify community composition across large areas, but with diverse effects on local food web structure. This result cautions against using the 'space-for-time approach' (Blois et al. 2013) when predicting future changes in food web structure, because drivers of spatial changes might be different from the drivers of temporal dynamics.

In our dataset, the temporal variability of community composition and food web structure was relatively weaker compared to the magnitude of spatial changes. Yet, these temporal changes can drastically alter locally adapted biotic communities. The strong spatial gradient was reinforced by the maximum diversity sampling strategy of the GSBTS, which selected the different Boxes to represent different environmental conditions (Ehrich et al. 2007). Using longer time series might help identifying stronger temporal dynamics. However, the relatively weaker temporal patterns compared to spatial patterns has been previously confirmed using a 30-year time series on fish communities in the North Sea (Frelat et al. 2017). The temporal scale might in fact have a counter-intuitive impact on food web structural changes, with stronger impact observed at finer temporal scales (CaraDonna et al. 2021). For instance, strong dynamics were reported for ecological networks at fine temporal scales (from hours to months) (Fründ et al. 2011), whereas general stability was found at broader scales (centuries and beyond) (Dunne et al. 2008).

In this study, node-weighted metrics often had similar scores to their unweighted counterparts, indicating that structural properties varied both qualitatively (in terms of species occurrence) and quantitatively (in terms of relative species abundance). However, in another study on the Baltic Sea, node-weighted metrics were complementary to unweighted and link-weighted metrics for describing temporal changes in food web structure (Kortsch et al. 2021). Therefore, we recommend using multiple approaches to capture a more complete picture of structural community changes. For instance, interaction strengths may be important for detecting structural and functional changes over time (Staniczenko et al. 2017, Kortsch et al. 2021), but evaluating interaction strength comes with additional data requirements and modeling assumptions. Our list of macroscopic structural metrics (i.e. indicators to characterize the whole food web) could also be complemented by microscopic metrics (characterizing the role of each taxa) or by motifs (characterizing the frequency of small building blocks) which may exhibit stronger spatio–temporal variability (Trøjelsgaard and Olesen 2016). Due to the complexity of our methodological framework, the interpretation of the results must be sequential and can rapidly become complicated if spatial components and the temporal components are entangled. Yet, we believe that PTA shows high similarity with the well-known PCA which may facilitate its adoption by ecologists.

By combining ecological network analysis with advanced multivariate analysis, we propose a framework to quantify and relate spatio–temporal changes in food web structure to changes in community composition. Our methodological approach can readily be used in areas where long-term monitoring of multiple trophic groups is carried out synchronously in order to support effective management strategies aimed at conserving the structure and functioning of ecological communities in times of environmental changes and species' distributional shifts.

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Author contributions

Romain Frelat: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Susanne Kortsch**: Conceptualization (supporting); Data curation (supporting); Supervision (equal); Validation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Ingrid Kröncke**: Conceptualization (supporting); Investigation (equal); Resources (supporting); Writing – review and editing (supporting). **Hermann Neumann**: Conceptualization (supporting); Data curation (supporting); Investigation (equal); Resources (supporting); Validation (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Marie C. Nordström**: Conceptualization (supporting); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Pierre E. N. Olivier**: Conceptualization (supporting); Data curation (supporting); Writing – review and editing (supporting). **Anne F. Sell**: Conceptualization (supporting); Data curation (supporting); Investigation (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (supporting); Writing – review and editing (supporting).

Transparent Peer Review

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Data availability statement

We provide the community composition, the metaweb, as well as the scripts to compute the food web metrics, the tensor decompositions and the co-inertia analysis in a companion GitHub repository (<https://github.com/rfrelat/NorthSeaFoodWeb>) and the Zenodo repository (<https://doi.org/10.5281/zenodo.4818058>). To accompany the openly available documented script, we also provide a tutorial on a single PTA on Zenodo (<https://doi.org/10.5281/zenodo.831740>) to encourage exploration of the PTA framework.

Supporting information

The supporting information associated with this article is available from the online version.

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