ECOGRAPHY

Research

Food-web structure varies along environmental gradients in a high-latitude marine ecosystem

Susanne Kortsch, Raul Primicerio, Michaela Aschan, Sigrid Lind, Andrey V. Dolgov and Benjamin Planque

S. Kortsch (http://orcid.org/0000-0002-6495-4781) (susanne.kortsch@abo.fi), R. Primicerio and M. Aschan, Norwegian College of Fishery Science, UiT, The Arctic Univ. of Norway, Tromsø, Norway. SK also at: Environmental and Marine Biology, Faculty of Science and Engineering, Åbo Akademi Univ., Turku, Finland. – S. Lind and B. Planque, Inst. of Marine Research, Langnes, Tromsø, Norway. – A. V. Dolgov, Knipovich Polar Research Inst. of Marine Fisheries and Oceanography, Murmansk, Russia.

Large-scale patterns in species diversity and community composition are associated with environmental gradients, but the implications of these patterns for food-web structure are still unclear. Here, we investigated how spatial patterns in food-web structure are associated with environmental gradients in the Barents Sea, a highly productive shelf sea of the Arctic Ocean. We compared food webs from 25 subregions in the Barents Sea and examined spatial correlations among food-web metrics, and between metrics and spatial variability in seawater temperature, bottom depth and number of days with ice cover. Several food-web metrics were positively associated with seawater temperature: connectance, level of omnivory, clustering, cannibalism, and high variability in generalism, while other food-web metrics such as modularity and vulnerability were positively associated with sea ice and negatively with temperature. Food-web metrics positively associated with habitat heterogeneity were: number of species, link density, omnivory, path length, and trophic level. This finding suggests that habitat heterogeneity promotes food-web complexity in terms of number of species and link density. Our analyses reveal that spatial variation in food-web structure along the environmental gradients is partly related to species turnover. However, the higher interaction turnover compared to species turnover along these gradients indicates a consistent modification of food-web structure, implying that interacting species may co-vary in space. In conclusion, our study shows how environmental heterogeneity, via environmental filtering, influences not only turnover in species composition, but also the structure of food webs over large spatial scales.

Keywords: biogeography, Barents Sea, Arctic

Introduction

It is well established that species' diversity and composition vary along environmental gradients (Worm and Myers 2003, Tittensor et al. 2010, Blois et al. 2013), but the implications of these patterns for food-web structure remain unclear (Cirtwill et al. 2015, Morris et al. 2015). To date, most large-scale spatial studies of ecological interactions are performed on relatively few (i.e. two or three) interacting species, functional

groups or food-web compartments (Worm and Myers 2003, Boyce et al. 2015a). Empirical studies of the spatial variation of highly resolved food webs are relatively rare (Poisot et al. 2015). The available studies have mainly addressed terrestrial bipartite networks (Kissling and Schleuning 2015, Morris et al. 2015, Trøjelsgaard et al. 2015, Pellissier et al. 2017), and a few studies were performed on unipartite networks (Romanuk et al. 2005, Thompson and Townsend 2005, Baiser et al. 2012, Cirtwill et al. 2015), of which, to our knowledge, only two are marine (Wood et al. 2015, Gilarranz et al. 2016).

A main source of variation in food-web structure along environmental gradients is driven by turnover in species composition due to environmental filtering (Pellissier et al. 2017), and by trait matching between co-occurring species (Tylianakis and Morris 2017). In the marine environment, temperature is one of the main drivers of species' distribution (Tittensor et al. 2010, Boyce et al. 2015b). Some of the most important traits determining food-web structure are body size, motility and thermoregulation, i.e. endothermism vs. ectothermism (Eklöf et al. 2013), which are dependent on water temperature (Gillooly et al. 2001, O'Connor et al. 2009, Soberón and Nakamura 2009). In aquatic food webs, body size is an important trait because feeding relationships are highly size-structured (Romanuk et al. 2011). Consumers are mostly larger than their prey, as observed in both plankton and fish communities, and larger organisms have a higher trophic level and are more prone to omnivory and generalism (Jennings and Mackinson 2003). In addition to select for specific traits, environmental conditions may also influence food-web structure via effects on whole community diversity and trophic complexity, for example along productivity gradients (Neutel et al. 2007), where trophically more complex communities (e.g. species-rich, link-rich, with many trophic levels and long path lengths) develop under adequate supply and availability of resources.

One way to compare food-web structure is from a network perspective (Dunne 2009). The spatial variation in food web configuration along environmental gradients can be assessed by comparing metrics describing relevant structural properties affected by the composition of species and their trait attributes (Tylianakis and Morris 2017). For example, the presence of large, generalist species will affect the connectivity and the modularity of a food web (Kortsch et al. 2015). Further, by relating interaction turnover to species turnover, the spatial component of food web variability can be explicitly addressed (Poisot et al. 2012). Previous studies have shown that interaction turnover is positively related to species composition and geographic distance (Poisot et al. 2012, Trøjelsgaard et al. 2015).

Marine ecosystems that display strong environmental gradients associated with variation in community structure are particularly suitable for investigating spatial variability in food-web structure. The Barents Sea is a shelf sea of the Arctic Ocean with large-scale gradients in temperature, salinity, depth and sea-ice coverage, and clear biogeographic patterns

in species' composition and diversity (Certain and Planque 2015, Fossheim et al. 2015). These gradients in hydrography are linked to productivity, where the warmer and nutrient-rich Atlantic waters of the southwest are more productive than the colder and ice-covered Arctic waters in the northeast (Reigstad et al. 2011). The resulting spatial variability in environmental conditions has strong structuring effects on fish and benthic communities (Johannesen et al. 2012, Aschan et al. 2013, Degen et al. 2016), leading to different food-web structures (Kortsch et al. 2015). Owing to these distinct subdivisions in species composition, the Barents Sea is a suitable ecosystem to investigate spatial variation in trophic interactions, i.e. food-web structure, along environmental gradients.

In the present study, we investigate large-scale variation in food web structure along environmental gradients across the Barents Sea. To compare the network properties of 25 subregions within the Barents Sea we rely on gradient and interaction turnover analyses using extensive ecosystem survey data and a highly resolved food-web dataset (Michalsen et al. 2011, Planque et al. 2014). We hypothesize that food-web structure varies across the Barents Sea, reflecting different climatic conditions and biogeographic regions. Specifically, we expect that the warmer, more productive south-western region of the Barents Sea is positively associated with fundamental food-web complexity metrics such as number of species (Duffy et al. 2017), connectance (Neutel et al. 2007), trophic levels (Arim et al. 2007), path length (Kaunzinger and Morin 1998, France 2012), and omnivory (Young et al. 2013). This is because these warmer and more productive waters can sustain a higher number of species with traits such as high motility and large body size and feeding strategies such as omnivory and generalism, features that likely require high resource availability (Wootton 2017). We also expect that the colder, ice-covered and less productive Arctic waters are negatively associated with the above-mentioned food-web metrics. Due the resulting limited food supply, the expected lower trophic complexity in Arctic waters follows from reduced growth and the selection of smaller body size in Arctic fish, which serve as important links between lower and higher trophic levels in aquatic food webs. Furthermore, number of species, link density, trophic level and path length are expected to be positively correlated with habitat heterogeneity, because more structurally complex habitats provide a greater diversity of niches in terms of habitat and diet, promoting community diversity (MacArthur and MacArthur 1961, Tews et al. 2004).

Material and methods

The Barents Sea

The Barents Sea is a high-latitude marine ecosystem characterized by a biogeographic divide with boreal (i.e. Atlantic) species in the southwest and Arctic species in the north and

northeast (Jørgensen et al. 2015, Johannesen et al. 2016). The bathymetry of the Barents Sea, the largest and deepest marginal shelf sea of the Arctic Ocean (Fig. 1a), is complex due to banks, trenches and steep shelf slopes (Fig. 1b; Supplementary material Appendix 1 Fig. 1a). The southwest region of the Barents Sea is strongly influenced by the inflow of relatively warm and saline Atlantic water (temperature > 3°C; salinity > 35.0 psu) (Ingvaldsen et al. 2002), whereas
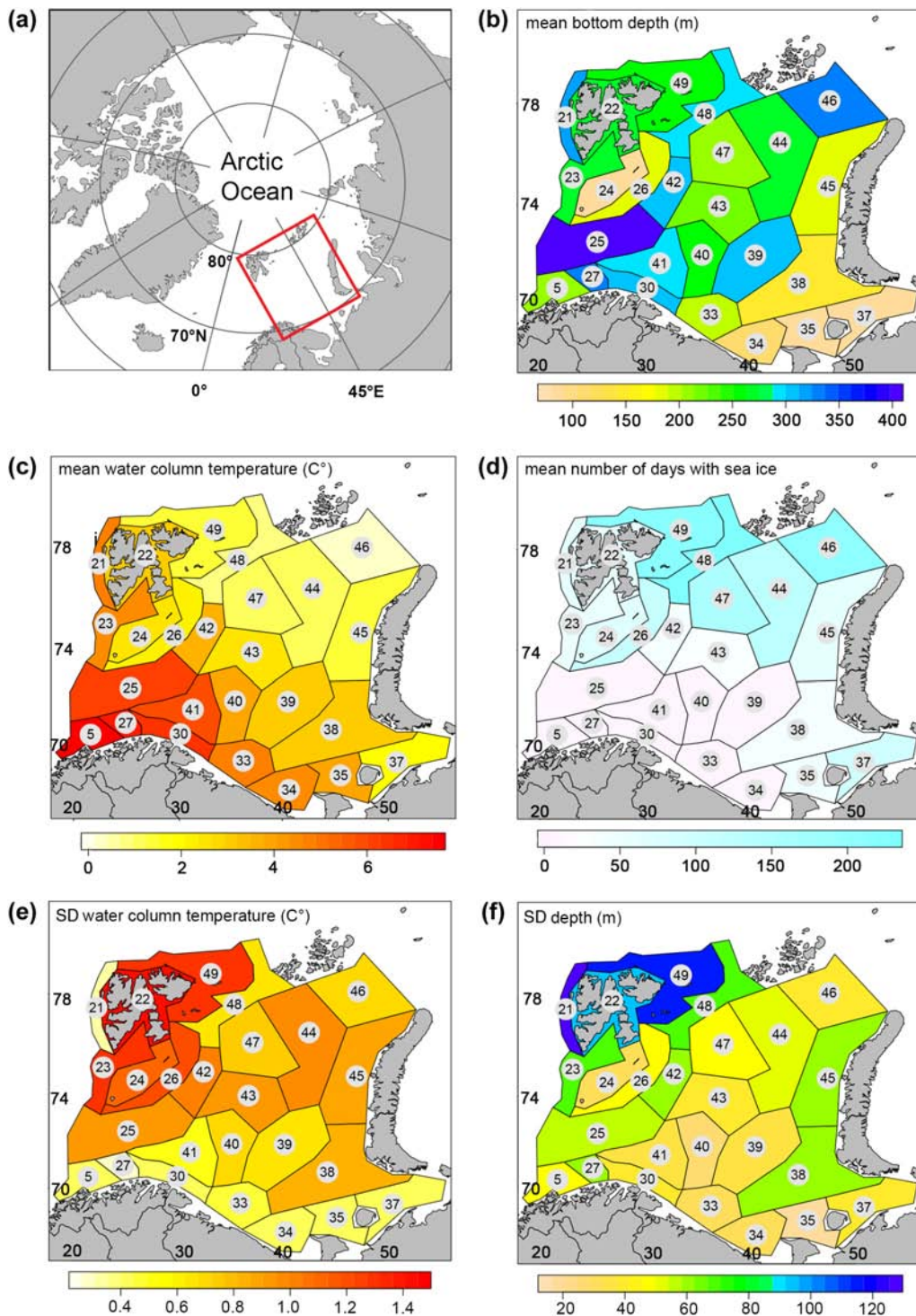

Figure 1. (a) Map of the Arctic Ocean and its bordering shelf seas. The location of the Barents Sea is indicated with a red square. The Barents Sea was divided into 25 sub-regions, i.e. polygons. Environmental information was retrieved for each polygon: (b) mean bottom depth (m); (c) mean water column temperature (°C) from the surface to the bottom layer; (d) the mean annual number of days with ice cover; (e) standard deviation of water column temperature and (f) standard deviation of bottom depth within polygons. The polygon id numbers are printed on top of each polygon region. The polygon ids are adapted from Hansen et al. (2016).

the northern Barents Sea is a typical stratified Arctic environment with colder and fresher Arctic water masses occupying the upper part of the water column (temperature < 0°C; salinity 34.0 to 34.7 psu), above a deep layer of modified Atlantic water (Lind and Ingvaldsen 2012, Lind et al. 2016) (Fig. 1c; Supplementary material Appendix 1 Fig. 1b). The Atlantic and Arctic water masses are separated by the Polar Front, a dominant hydrographic feature in the upper layers (Loeng 1991) (Supplementary material Appendix 1 Fig. 1a, b). The Polar Front is largely topographically controlled and stationary in the western Barents Sea, but more variable in the east, where its position is largely determined by the interannual variability of the Atlantic water inflow (Loeng and Drinkwater 2007). The region north/north-east of the Polar Front has seasonal ice cover, strongly influencing biological production (Dalpadado et al. 2014) (Fig. 1d). At present, the Barents Sea is experiencing some of the greatest losses of sea ice and surface warming in the Arctic, especially along the marginal ice zone in the northeast (Carmack et al. 2015), including a warming of the entire water column (Lind and Ingvaldsen 2012). Further details on the hydrography of the Barents Sea and the selected environmental variables are presented in the Supplementary material Appendix 1 Fig. 1–3).

Food webs

Food webs are representations of trophospecies (i.e. groups of organisms sharing the same predators and prey) and their trophic interactions. The terms trophospecies, species, and taxa will be used somewhat interchangeably in this paper. To study how food-web structure varies across the entire Barents Sea ecosystem, we compiled 25 food webs for chosen subregions delimited by polygons (Supplementary material Appendix 1 Fig. 1c). The boundaries of the polygons are to a large degree defined by the topography and enclose relatively homogenous areas with respect to hydrography and bathymetry (Hansen et al. 2016), two features known to influence species' distribution in the Barents Sea. The 25 subregional food webs were constructed by selecting the trophospecies present in each polygon based on information from a large-scale ecosystem survey taking place in the late summer period (August/September), covering the entire Barents Sea. The corresponding feeding links were sub-sampled from the Barents Sea food-web database (Planque et al. 2014). A diagrammatic description of how we subsampled the food webs within subregions is shown in Fig. 2. The metaweb database includes the most common taxa from the seafloor to the surface across the entire Barents Sea, comprising 233 trophospecies and 2218 feeding links. When assembling the 25 regional food webs, we assumed that species co-occurring in a polygon (i.e. subregion) and connected via trophic interactions in the metaweb also interact within the polygon. Further details on the Barents Sea ecosystem survey and the Barents Sea food web are presented in the Supplementary material Appendix 2 Fig. 1 and 2).
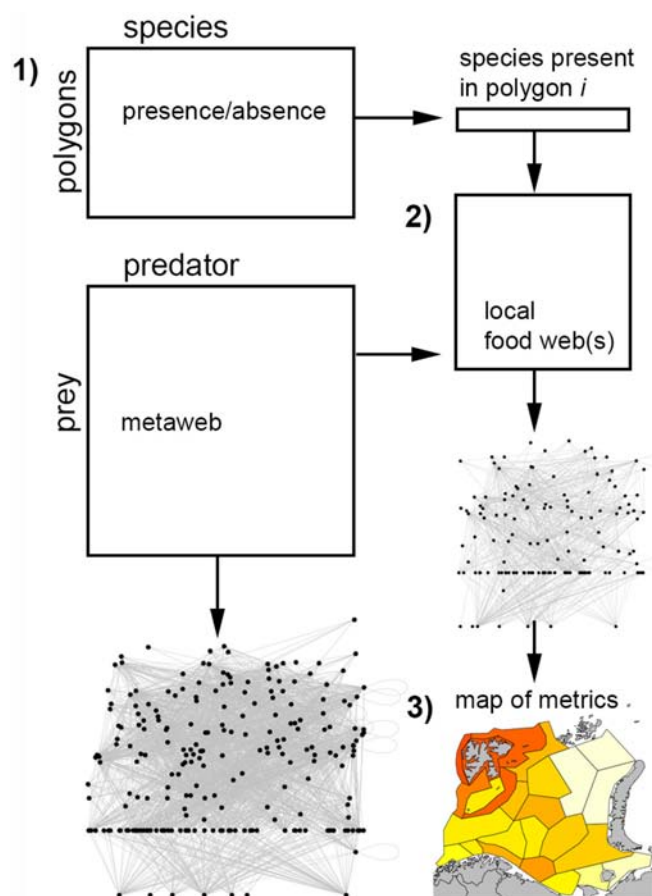

Figure 2. Diagrammatic description of the food-web subsampling procedure. 1) We used a polygon-by-species matrix together with the metaweb food web for the entire Barents Sea to subsample feeding links used to generate food webs within polygons. 2) The food webs within polygons were used to calculate the food-web metrics. 3) The metric values were colour coded and plotted for each polygon/food web in space.

Strengths and limitations of the Barents Sea food-web data set

Topological food-web descriptions are static representations of species' trophic interactions. In nature, however, food webs are dynamical and food-web configurations vary in time and space. The food webs in this study are representative for the late summer (August/September) period in the Barents Sea, when sea ice is at its minimum, most marine organisms are intensively foraging and the distribution of boreal foraging migrants is widest (e.g. cod *Gadus morhua*). Highly mobile migrating taxa (e.g. large fish, sea birds and marine mammals) change their distribution throughout the year; hence, food-web structure will vary seasonally, a factor that cannot be accounted for in our approach. Species connected in the metaweb are assumed to be connected also in the sub-webs (i.e. polygon food webs) if both species co-occur, assuming interactions that may not be realized. We acknowledge the limitations of our assumptions, and recognise that our results

do not fully represent realized food-web structures in space and time, but give a reliable representation of the potential food-web structures in space for the summer/autumn conditions for the period 2004–2007 in the Barents Sea. A strength of our study is that, unlike most comparative food-web studies, food webs for the different regions were compiled with identical methodology and from a common data source. This implies that dissimilarities observed between the 25 food webs should be attributed to differences in species composition and link configuration of the food webs among regions, and not to differences in the classification and aggregation of trophospecies. Further details on the construction of the Barents Sea metaweb are presented in Planque et al. (2014).

Food-web metrics

To characterize the topological structure of regional food webs, we selected 18 food-web properties commonly addressed by topological food-web analyses: 1) number of species, 2) number of links, 3) link density, 4) directed connectance, 5) modularity, 6) clustering, 7) level of omnivory, 8) proportion of omnivores, 9) proportion of cannibals, 10) predator per prey, 11) prey per predator, 12) mean short-weighted (sw) trophic level, 13) mean shortest path length, 14) proportion of basal species, 15) proportion of intermediate species, 16) proportion of top species, 17) vulnerability SD, i.e. standard deviation of the out-degree distribution, and 18) generality SD, i.e. standard deviation of the in-degree distribution. Apart from the fundamental metrics of food web complexity such as number of species and connectance, our discussion focuses on a subset of metrics such as the level of omnivory and trophic level that are important features of aquatic food webs (Dunne et al. 2004, Thompson et al. 2007), and therefore particularly relevant to detect structural variation along environmental gradients in marine systems. We also included degree of modularity to characterize how densely sub-groups of species interact with one another compared to species from other sub-groups (Newman and Girvan 2004). Definitions and some known dynamical implications of the chosen metrics are presented in more detail in Table 1.

Environmental data

To relate food-web structure to marine environmental conditions, we retrieved the following environmental data for each polygon (Fig. 1b–f): mean temperature from surface to bottom, mean number of days with sea ice cover, and mean bottom depth. To assess the associations between food-web structure and environmental variables, we chose environmental variables with known effects on species composition in the Barents Sea (Johannesen et al. 2012, Fossheim et al. 2015, Jørgensen et al. 2015, Degen et al. 2016). Heterogeneity in the physical habitat was estimated using the standard deviation of bottom depth and temperature within each polygon. Bottom depth was registered by depth sensors for each bottom-trawl station. Following an approach by Lind et al.

(2016), ocean temperature and salinity observations from conductivity-temperature-depth profiles, sampled during the joint Norwegian–Russian ecosystem surveys in August and September during 2004–2007, were interpolated on horizontal grids with a high vertical resolution, see Supplementary material Appendix 1 for details. Mean temperature and salinity, and corresponding standard deviations, were estimated for the whole water column in each polygon from the gridded fields (Supplementary material Appendix 1 Fig. 1b and 2). The sea-ice data were gridded SMMR and SSM/I passive microwave data with 25 × 25 km resolution obtained from the National Snow and Ice Data Centre (Maslanik and Stroeve 1999, Meier et al. 2006). The total number of days with more than 15% sea ice concentration in August 2004– July 2007 was assigned to each trawl station and averaged over each polygon.

Exploitation (i.e. fisheries) affects marine ecological systems directly (Gislason and Sinclair 2000) or in conjunction with environmental variation (Planque et al. 2010), and is thereby a potential confounding factor in the context of our study. But fishing pressure could not be included as a covariate in our analyses due to the unavailability of appropriate geographical data on fishing effort at the scale of the Barents Sea shelf. The analyses presented here rely exclusively on presence/absence data. Given that exploitation in the Barents Sea does not drive species to extinction, it is assumed that the effects of exploitation on the food-web structures identified with the present approach would be small relative to the effects of the chosen environmental variables.

Null model of spatial food-web structure

To determine if the observed patterns in food-web structure are associated with environmental gradients, we compared the empirical food-web metrics to those obtained from null model simulations. The purpose of the null model is to explore whether the spatial food-web patterns are informative or whether they could have emerged by chance. In the null model, spatial variation in food-web structure results from random distribution of species under few constraints. The alternative hypothesis is that spatial variation in food-web structure is environmentally driven, rather than resulting from random species distribution. Simulated food webs were constrained to preserve four properties of the empirical food webs: 1) the frequency of occurrence of species at the scale of the Barents Sea (i.e. if a species is present in e.g. five polygons, it is also present in five polygons in the null-model simulations), 2) the number of species in each polygon, 3) the connectivity of species (i.e. no species should be disconnected from the rest of the food web), 4) non-basal species must have at least one prey item. In the empirical data set, there are five polygons in which one species (either *Aglantha digitale* or *Arctozenus risso*) is not linked to a prey item, and we therefore allowed that one non-basal species could be present without a prey in the randomised food webs.

Simulated food webs were constructed by randomising the species-by-polygon matrix using the swap algorithm

Table 1. List of metrics, their definition and potential associated structural and dynamical implications in an ecological context.

Metric	Defintion	Structural and dynamical implications	References
Number of species	Number of taxa (nodes) in a food web.	Species diversity has implications for the persistence of ecosystems, and may show decreased stability at the population level but increased stability at the community level. Species diversity may reflect combined effects from underlying ecological processes such as productivity and stability.	May 1973, Tilman 1996
Number of links	Number of trophic interactions in a food web.	Link richness has implications for the complexity of the food web, and the number of pathways along which energy can flow.	Dunne et al. 2002
Link density	Number of trophic interactions (links) per species.	The average number of links per species informs about how connected species are within the food web.	Dunne et al. 2002
Connectance	Directed connectance describes the proportion of directed links realized out of the maximum number of possible links.	Connectance is a fundamental measure of network complexity. Connectance can be negatively or positively associated with food-web robustness, depending on the network structure (random vs non-random) or how the strength of the interactions are distributed.	May 1973, Dunne et al. 2002
Modularity	Modularity describes how densely sub-groups of species interact with one another compared to species from other sub-groups.	Modularity is positively associated with robustness, because perturbations can be retained within modules, preventing them to spread to the whole network.	May 1973, Stouffer and Bascompte 2011
Clustering	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. Similarly to connectance, clustering may influence the stability of the food web.	Montoya and Solé 2002
Level of omnivory	Level of omnivory of each species is the standard deviation of the short-weighted trophic level of its resources.	Omnivory can negatively or positively influence the stability of communities, depending on the interaction strength. Intermediate levels of omnivory may stabilize communities, and may diffuse top-down influences through the food webs and thereby reduce the probability of trophic cascades.	McCann and Hastings 1997, Bascompte et al. 2005, Wootton 2017
Proportion of omnivores	Proportion of taxa that feed on resources on more than one trophic level.	A higher the proportion of omnivores increases the probability for omnivory. As food chains lengthen and trophic levels increase, omnivory becomes increasingly prevalent.	Thompson et al. 2007
Proportion of cannibals	Proportion of taxa that feed on themselves.	Moderate levels of cannibalism e.g. in fish, can reduce inter-cohort competition, enabling coexistence of many cohorts, but it can also be destabilizing and lead to alternative stable states.	Claessen et al. 2000
Predators per prey	The mean number of predators per prey.	The more predators a prey species has, the higher the out-degree, the more vulnerable it becomes to predation.	Dunne 2009
Prey per predator	The mean number of prey per predator.	The more prey a predator sepcies has, the higher the in-degree, the more generalist it becomes.	Dunne 2009
Short-weighted (sw) trophic level	Mean of all short-weighted paths from base to each species.	The number of trophic levels is a central feature of the vertical structure of food webs and is related to the length of food chains. The height of trophic levels reflects ecological processes that sustain top predators.	Thompson et al. 2007
Mean shortest path length	Mean shortest food chain connecting each pair of species in a food web.	The stability of food chains depends on their length. Short chains are shown to be more stable than long chains. Food chains may lengthen in more productive ecosystems.	Kaunzinger and Morin 1998, Borrelli and Ginzburg 2014
Proportion of basal species	Proportion of taxa with no prey.	The proportion of basal species is often under-represented in marine food webs. The few basal species impart a funnel shape at the base of the food web.	Kortsch et al. 2015
Proportion of intermediate species	Proportion of taxa that are both prey and predators to other species.	The proportion of intermediate species influence the connectivity of a food web between lower and upper trophic levels. The proportion of intermediate species is positively associated with connectance and level of omnivory.	Dunne et al. 2004, Romanuk et al. 2005
Proportion of top species	Proportion of taxa with no predators.	Top predators may induce indirect, top down effects such as trophic cascades through lower trophic levels.	Frank et al. 2005
Vulnerability SD	Normalized standard deviation of vulnerability (i.e. number of consumers per taxon) in the food web.	Higher VulSD reflects the variability in the out-degree distribution.	Dunne 2009
Generality SD	Normalized standard deviation of generality (i.e. number of resources per taxon) in the food web.	Higher GenSD reflects the variability in the in-degree distribution.	Dunne 2009

proposed by Strona et al. (2014). A graphical description of the null-model computation procedure is presented in the Supplementary material Appendix 3 Fig. 1. In the swap algorithm, the number of species in each polygon is preserved, as well as the number of polygons in which a given species occurs. We used the new, randomized list of species for each polygon to generate 'null' food webs by subsampling the trophic interactions of the randomized species lists from the metaweb. We retained simulated food webs that satisfied all the four constraints specified above. The procedure was reiterated until 9999 randomized food webs were obtained for each polygon, and these were then used to compute the null distribution for each metric. Empirical values of food web metrics were considered to deviate strongly from the randomized food webs if these were outside the 0.05 to 0.95 quantile range of the null distribution. For each polygon, the probabilities of the empirical values under the null model are reported in italics on the maps in Fig. 3. A table with the null model outputs is presented in the Supplementary material Appendix 3 Table 1.

Data analyses

To group the polygons into main regions with similar food-web characteristics, we applied hierarchical clustering based on Euclidian distances and ward linkage on the food-web metrics (Ward 1963). Ward clustering emphasizes sharp differences between, and strong homogeneity within, clusters. In our map, we highlighted clustering based on a specific cut level of the dendrogram chosen based on the configuration of distances between food webs (Supplementary material Appendix 4 Fig. 1 and 2). To examine the most important correlations among the food-web metrics and the chosen environmental variables across polygons, we applied a redundancy analysis (RDA, Legendre and Legendre 1998). The environmental variables included in the RDA were mean bottom depth and water column temperature, and standard deviation of bottom depth and water column temperature (Fig. 1b, c, e, f). Due to collinearity between temperature and sea-ice coverage, the food-web data was not constrained by the latter (Fig. 1d), and sea-ice coverage was displayed only as a passive variable. The significance of the RDA result was tested by permutation.

To assess the relationship between species turnover and interaction turnover along environmental gradients, we calculated the beta dissimilarity (β) for species composition and network structure between pairs of food webs for all pairwise combinations of the 25 Barents Sea food webs. To compute the beta dissimilarities, we used the beta diversity (β_w) measure by Whittaker (1960).

Beta dissimilarity (β_w) was computed as

$$\beta_w = \frac{a+b+c}{(2a+b+c)/2} - 1$$

where a is the number of items (e.g. number of species or number of interactions) shared between network A and B, b is the number of items unique to network A and c is the number of items unique to network B. The interaction turnover was further related to spatial and environmental distance between polygons. The geographic distance (km) was calculated as the distance between the midpoints of the polygons, and the difference in environmental characteristics between polygons was derived from a principal component analysis (PCA) of the environmental variables.

All computations and statistical analyses were performed in R, ver. 3.2.1 (R Core Team). Modularity was calculated with the spinglass algorithm using the igraph package (Csardi and Nepusz 2006). The multivariate analyses were performed with the statistical packages vegan and Pvclust (Suzuki and Shimodaira 2006, Oksanen et al. 2007). Beta dissimilarity was computed using the betalink package (Poisot et al. 2015).

Data deposition

The food-web dataset files used in this study can be downloaded from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k04q2kd> (Kortsch et al. 2018). The R codes used in this study can be made available to readers upon request.

Results

Spatial patterns in food-web metrics across the Barents Sea

Network analyses revealed considerable variability in food-web metrics across the Barents Sea, with distinct large-scale biogeographic patterns (Fig. 3). Based on hierarchical clustering, the Barents Sea was divided into four main regions (Fig. 4a): the southwest-central (boreal; 10 subregions), the Svalbard Archipelago (4 subregions), the northeast (Arctic; 3 subregions), and the southeast-shallow water (8 subregions), the latter also included three polygons (24, 47 and 48) to the north. Among the four clusters, the northeast Arctic food webs displayed the most distinct characteristics in network topology compared to the remaining food webs (Supplementary material Appendix 4 Fig. 2). The Arctic food webs in the northeast Barents Sea stood out with significantly higher modularity, predators per prey, proportion of top species and standard deviation of vulnerability than expected from the null model (Fig. 3e, j, o, p). In contrast, the number of links, connectance, proportion of omnivores, proportion of cannibals, mean sw trophic level, and proportion of intermediate species were significantly lower in the northeast than expected from the null model (Fig. 3b, d, h, i, l, n). The boreal food webs of the southwest and central Barents Sea, influenced by warmer Atlantic water, were positively associated with link density, connectance, clustering, proportion of cannibals, level of omnivory, and mean sw trophic level (Fig. 3c, d, f, g, i, l), whereas modularity and vulnerability SD were low (Fig. 3e and p). The most complex food webs, in terms of species and link density, were found in the Svalbard archipelago (Fig. 3a, b, c). These food webs were also

characterized by a high proportion of omnivores, many prey per predator, higher trophic levels, higher proportion of intermediate species, and longer mean shortest paths (Fig. 3h, k, l, n, r). The southeast-shallow water food webs were positively associated with connectance, prey per predator, proportion of intermediate species, and generality SD (Fig. 3d, k, n, q). A summary table of the null model results are presented in the Supplementary material Appendix 3 Table 1.
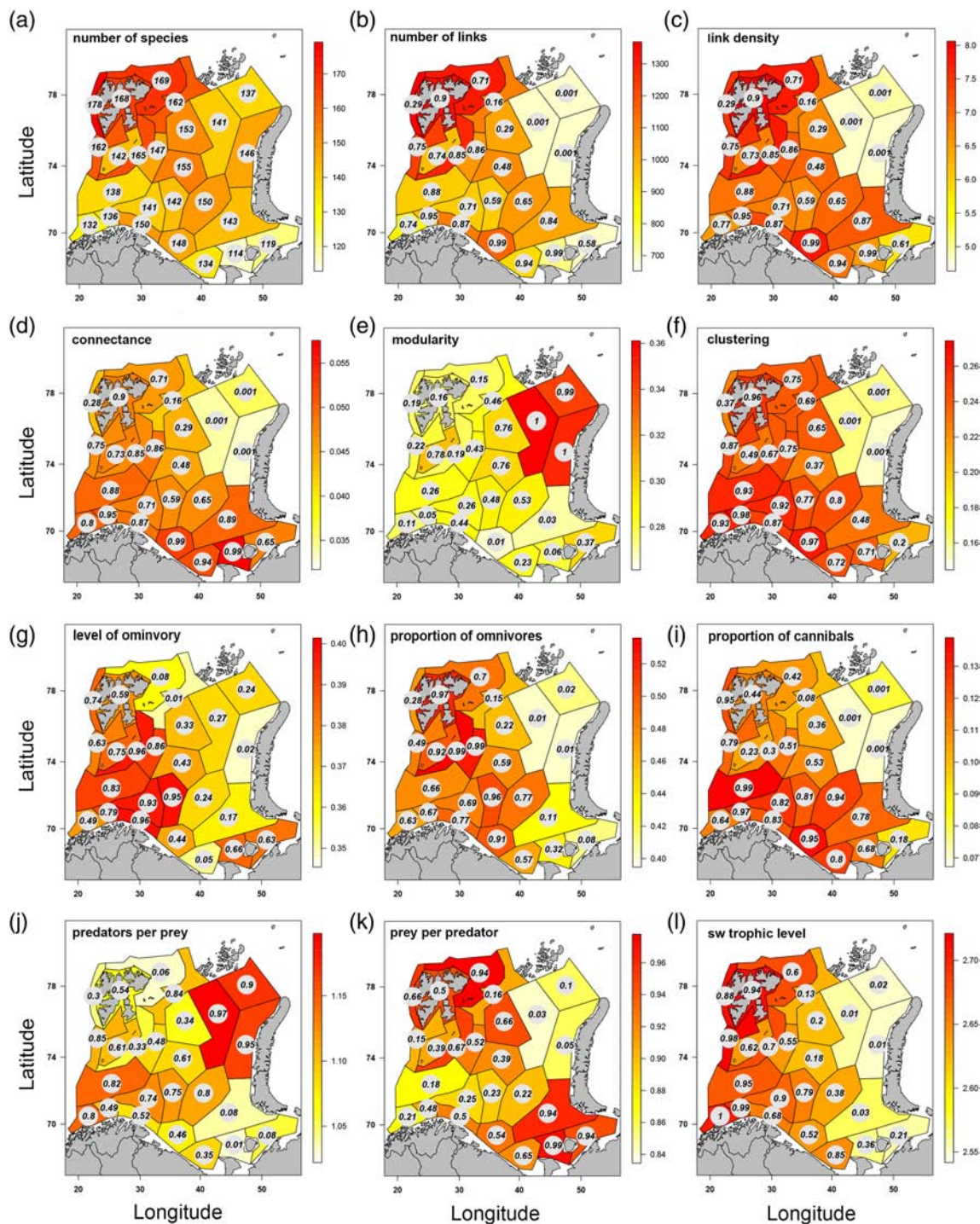

Figure 3. Spatial variation in selected food-web metrics: (a) number of species; (b) number of links; (c) link density; (d) connectance; (e) modularity; (f) clustering; (g) level of omnivory; (h) proportion of omnivores; (i) proportion of cannibals; (j) predators per prey; (k) preys per predator; (l) short-weighted trophic level; (m) proportion of basal species; (n) proportion of intermediate species; (o) proportion of top species; (p) vulnerability SD; (q) generality SD; (r) mean shortest path length. The gradient bar to the right of each panel provides a legend for the empirical food-web estimates. The null model probabilities are printed with italic numbers on top of each polygon. Null model probabilities ≤ 0.05 or ≥ 0.95 indicate that the empirical food-web values deviate strongly from the null model expectation.
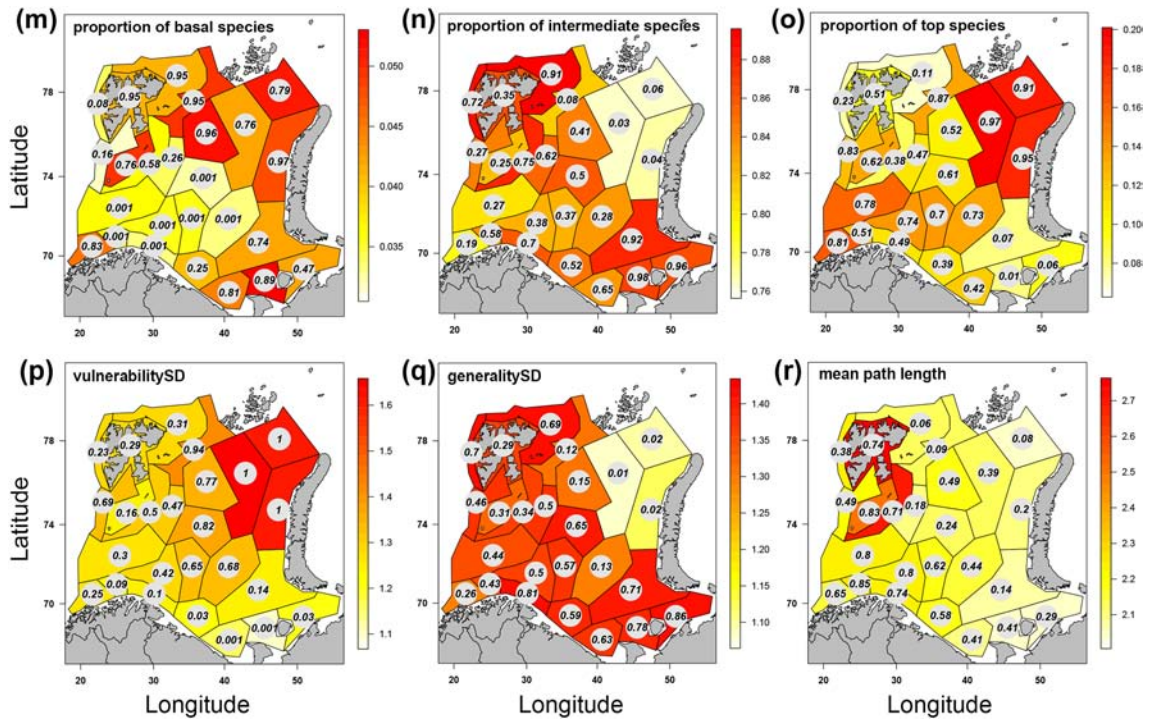
Figure 3. (Continued).

Association between food-web metrics, environmental drivers and habitat heterogeneity

The first and second axes of the RDA accounted for 26 and 10%, respectively, of the constrained variation in the food-web data (Fig. 4b), and indicated that warmer and ice-free waters were positively associated with connectance, clustering, proportion of cannibals and level of omnivory (boreal food webs displayed high values for these metrics, see light orange points in Fig. 4b). Sea ice cover and low temperatures were positively associated with higher modularity and vulnerability SD (Arctic food webs displayed high values for these metrics, see blue points in Fig. 4b). Environmental heterogeneity, i.e. standard deviation of bottom depth and water column temperature, was highest in the region surrounding the Svalbard archipelago (polygons 21, 22, 26 and 49) in the northwest. This coastal region has a highly varying hydrography due to mixing of warm saline Atlantic,
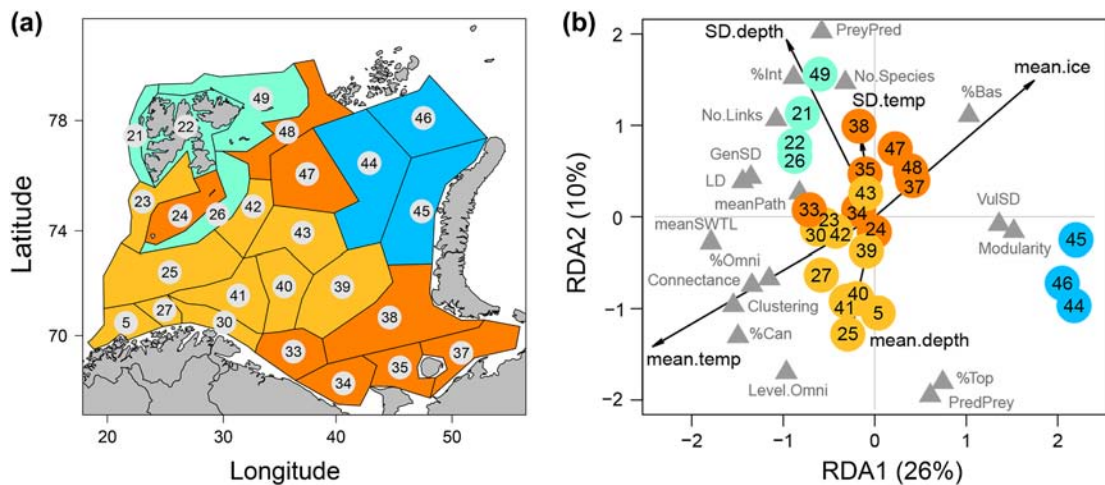

Figure 4. (a) The four main food-web regions of the Barents Sea are: the southwest and central (light-orange), the Svalbard Archipelago (green), the northeast Arctic (blue) and the southeast-shallow water (organge). (b) Tri-plot of redundancy analysis (RDA) results showing the relationship between sampled food webs (circles with polygon numbers are colored according to cluster affiliation), food-web metrics (grey triangles), and environmental variables (black arrows), mean temperature (mean.temp), standard deviation of temperature (SD.temp), mean depth (mean.depth) and standard deviation of depth (SD.depth). The mean days of ice cover was included as a passive variable in the RDA.

cold Arctic and costal water masses and a complex bathymetry due to fjords, shelves and steep shelf slopes (Fig. 1f). Habitat heterogeneity was positively associated with numbers of species, link density, prey per predator, sw trophic level and mean shortest path length (see light green points in Fig. 5b). A summary table of the RDA results and permutation test outcomes are presented in the Supplementary material Appendix 5 Table 1 and 2.

Relationship between species and interaction turnover

Turnover in trophic interaction increased with turnover in species composition (Fig. 5). The relationship had a steeper slope than 1, and for a given compositional dissimilarity, the interaction dissimilarity between food webs varied considerably. In addition, dissimilarity in species trophic interactions among Barents Sea food webs increased with geographical distance (Fig. 5 and Supplementary material Appendix 6), being highest for distances separating distinct climatic regions. The higher interaction turnover values for a given species turnover were consistently higher than those associated with the null-model food webs (Supplementary material Appendix 6 Fig. 1). Further, linear regression analyses (Supplementary material Appendix 6 Fig. 2a) showed that interaction turnover increased with geographic distance ($R^2 = 0.28$) and with environmental distance (Supplementary material Appendix 6 Fig. 3a, b) measured along the main environmental gradient PC1 ($R^2 = 0.21$).

Discussion

Biogeography of high-latitude marine food webs

In the Barents Sea, food-web metrics display systematic spatial variation along environmental gradients, separating
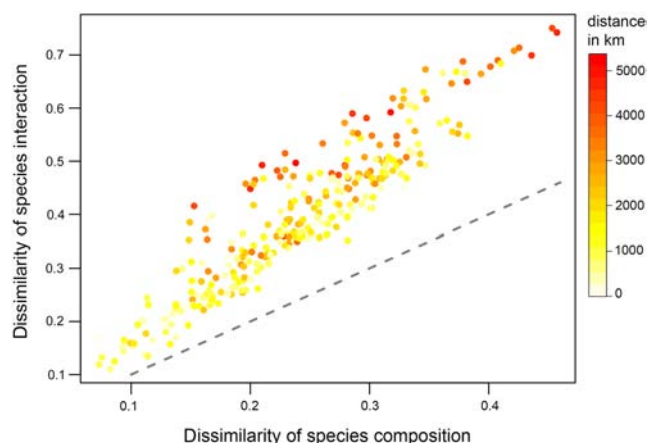

Figure 5. Relationship between interaction turnover and turnover in species composition for all possible pair-wise comparisons (300) among the 25 food-webs. The yellow to red colours of the circles indicate the geographic distance in kilometers between pairs of food webs, see color bar in legend. The dashed grey line indicates the 1:1 relationship.

distinct biogeographic regions. The division of the Barents Sea into four main regions sharing similar food-web characteristics mirrors previous biogeographic subdivisions of the Barents Sea, in particular along the southwest-to-northeast axis ranging from warmer Atlantic to colder Arctic waters (Fossheim et al. 2015, Jørgensen et al. 2015). The relationship between food-web configurations and environmental gradients suggests that broad-scale variation in species' spatial distributions, shaped by environmental filtering and by species' ecological niches (e.g. diet breadth), manifest themselves as distinct biogeographic patterns in food-web structure. In line with previous comparative multivariate studies of food webs, we find that link density and connectance are more important metrics than species richness in accounting for the structural variation among food webs (Vermaat et al. 2009, Baiser et al. 2012). Number of species is thereby not the primary driver of the geographic variation in food-web complexity in the Barents Sea, although it scales with number of links and connectance as observed in previous studies (Riede et al. 2010). Rather, structural differences in food-web topology, such as modularity, connectance and level of omnivory, across the Barents Sea are driven by the composition of species, and by their biological characteristics (e.g. size and motility) and network role (e.g. ecological niche breadth), leading to trophic link configurations that are region-specific.

However, for a given compositional dissimilarity (i.e. species turnover), nearby food webs have more similar interaction structure than geographically distant food webs, in line with previous studies (Poisot et al. 2015, Trøjelsgaard et al. 2015), and interaction dissimilarity is highest for geographic distances separating distinct climatic regions. The higher interaction turnover compared to species turnover along environmental gradients (i.e. the steeper than 1 slope) indicates a consistent modification of food-web structure along those gradients. Such a consistent variation in interaction turnover with distance along environmental gradients could indicate that interacting species co-vary along those gradients, implying that interacting species have similar responses to the environment, and/or that species interactions influence species distributions.

Food-web structure along environmental gradients

Species traits such as body size, motility and the degree of diet specialization are known to be good predictors of food-web structure (Polis et al. 1989, Eklöf et al. 2013). Body size, metabolism, and motility are all influenced by ocean temperatures and linked to resource demands (Gillooly et al. 2001, Tylianakis and Morris 2017). In the Arctic, growth is constrained by a limited energy supply due to cold seawater, the sea ice and the short productive season. Such environmental conditions select for reduced energy expenditure and result in small adult size in fish, which play an important role in coupling different compartments of aquatic food webs. As a consequence, fish in Arctic communities are generally smaller, more stationary and more closely associated with the seafloor

than fish in boreal communities (Wiedmann et al. 2014, Frainer et al. 2017, Marsh et al. 2017, Mecklenburg et al. 2018), which are more pelagic and motile (Fossheim et al. 2015). Considering that marine food webs are highly size-structured (Romanuk et al. 2011), these major differences in fish body size and motility between the boreal and the Arctic regions are expected to result in different link configurations, as we observe in the Barents Sea.

The main gradient of food-web variation in the Barents Sea spans along the southwest-to-northeast axis (i.e. the Atlantic to Arctic axis), and is associated with gradients in seawater temperature and sea ice. Arctic food webs in the northeast, which are associated with cold Arctic water masses and a seasonal ice cover, display the most distinct structure relative to the other regions. Despite the number of trophospecies being similar to that of other regions, these food webs contain relatively fewer links, resulting in fewer links per species, low connectance, and high modularity. This illustrates that relatively high diversity does not necessarily imply high trophic complexity. The lower trophic complexity in the Arctic can be ascribed to a relatively low proportion of intermediate hub species (i.e. species with many trophic links), which leads to a lower connectivity between higher and lower trophic levels (Dunne et al. 2004, Romanuk et al. 2005). This has been shown to increase the modularity of the Arctic Barents Sea food web (Kortsch et al. 2015). These food-web properties may reflect a wasp-waist shape of the Arctic food webs where only a few intermediate species, such as polar cod *Boreogadus saida* have a central role in controlling the dynamics of the trophic network (Hop and Gjøsæter 2013).

Wasp-waist food webs are primarily ascribed to highly productive upwelling systems (Cury et al. 2000), however, the Arctic Barents Sea food web is associated with relatively low annual productivity. The wasp-waist system of the Arctic may be a result of several processes. First, the ice-associated short but highly pulsed seasonal production in the spring leads to a rich detritivore-driven benthic environment in terms of diversity and biomass (Degen et al. 2016). Secondly, the coupled ice-land associated habitat hosts many top predators (i.e. sea birds, seals, walruses and polar bears) of which many are seasonal migrants, feeding on the lipid-rich pelagic production and the rich benthic biomass. On the other hand, the short productive season of the Arctic is not capable of sustaining a high pelagic production of fish at intermediate trophic levels, except for a few species such as polar cod. The high proportion of top predators but relatively few intermediate species with many in-going and out-going interactions give rise to the wasp-waist structure.

A main difference in food-web structure between the boreal (i.e. Atlantic) and Arctic regions has recently been explained by the greater occurrence of highly connected generalist fish in the boreal region, e.g. Atlantic cod and haddock *Melanogrammus aeglefinus*, and by the absence of these large, motile generalists in the Arctic region, except for Greenland halibut *Reinhardtius hippoglossoides* (Kortsch et al. 2015). These super-generalists are characterized by many trophic interactions, connecting species across habitats and trophic levels, which increases connectance but reduces modularity. The presence of species with a broad niche (high in-degree) also explains the high omnivory of the boreal region, corroborating predictions from a size-structured model showing that omnivory evolves in response to niche width and competition (Loeuille and Loreau 2005). Compared to fish species in boreal communities, typical Arctic fish have a more specialized benthic diet (e.g. *Lycodes* spp. and *Icelus* spp.), an observation supported by several Arctic studies from the northeastern Barents Sea and the Kara Sea (Dolgov 2014, Dolgov et al. 2014), and by a recent study from the high-Arctic Chukchi Sea (Marsh et al. 2017). The latter study shows that Arctic fish communities occupy a smaller isotopic niche space and specialize more on benthic prey, whereas warm-water fish have a broader isotopic niche and feed more in the pelagic compartment (Marsh et al. 2017), also in line with recent findings from the Barents Sea (Frainer et al. 2017). The Arctic region also shows lower omnivory and lower mean short-weighted trophic level, despite a high proportion of top predators, most likely due to fewer species with many trophic interactions at intermediate trophic levels.

Habitat heterogeneity promotes food-web complexity

Food-web complexity, in terms of number of species, number of links and link density, was positively associated with habitat heterogeneity, defined as within polygon variability in depth and water temperature, around the Svalbard archipelago. This finding supports a previous empirical study on aquatic food webs and the habitat heterogeneity hypothesis (MacArthur and MacArthur 1961, Thompson and Townsend 2005), stating that structurally complex, heterogeneous habitats provide a greater diversity of niches and availability of environmental resources promoting diversity (Tews et al. 2004). Indeed, a recent study on fish diversity patterns showed that the Svalbard region contained the highest diversity and turnover rates of fish in the Barents Sea (Certain and Planque 2015). The relatively high species diversity around Svalbard may be linked to the complex hydrography (i.e. mixing of Atlantic, Arctic and coastal water mases) and strong spatial variability in bathymetry, expanding the species pool, resources and niche diversity in terms of habitat and diet. Additionally, the inflow of nutrient-rich water and the relatively high pelagic productivity in this region (Degen et al. 2016) are conditions that may sustain high food-web complexity (i.e. high link density, high connectance, high mean path length).

Implications for the effects of climate change on Arctic marine food-webs

Given the observed variation in food-web structure along climatic gradients, a reorganisation of food-web configurations may be expected as a consequence of warming (Hattab et al. 2016, Pecl et al. 2017). However, it is notoriously hard to foresee how ecosystem structure, dynamics and

functioning will change in response to warming (Planque 2016). Nonetheless, information on changes that have occurred in recent decades due to warming and analyses that substitute space-for-time can provide some indication of how food webs may look like in a warmer Barents Sea. The northern part of the Barents Sea is among the regions in the Arctic undergoing some of the most extensive and rapid environmental changes driven by global warming with large reductions in the sea ice cover accompanied by substantial warming of the entire water column (Lind and Ingvaldsen 2012, Carmack et al. 2015, Lind et al. 2016). This has led to a rapid retraction of the marginal ice zone and a prolonged open-water season (Dalpadado et al. 2014, Carmack et al. 2015). The documented responses to this warming are increased pelagic primary and secondary production and a poleward movement of pelagic and generalist fish (Orlova et al. 2013, Dalpadado et al. 2014, Fossheim et al. 2015, Eriksen et al. 2016). Owing to the distributional shift of species, the structure of the Arctic food-webs is becoming more connected and less modular, in particular at intermediate trophic levels, with consequences for tropho-dynamics and ecosystem functioning (Kortsch et al. 2015, Frainer et al. 2017), possibly leading to a more extensive and rapid spread of energy, matter and pertubations. Given the observed changes in the Barents Sea, we hypothesise that food-web configurations such as omnivory, trophic loops, and longer food chains may become more prevalent in Arctic Barents Sea food webs as a result of a more trophically complex and species-rich pelagic food-web compartment, potentially leading to dynamically more unstable food-web configurations. However, the higher levels of omnivory could also stabilize Arctic food webs by diffusing top-down effects (Bascompte et al. 2005).

Concluding remarks

The structure of Barents Sea food webs varies systematically in space along environmental gradients known to filter species characteristics such as body size which, in turn, influence the structure of feeding relationships. Climatic constraints on fish body size (the Arctic fish being smaller than boreal fish) and their ecological niche space (Arctic fish being more specialized than boreal fish) result in regionally distinct food-web structures. Although the generality, or context-dependency, of our findings remains to be examined further, our study indicates that environmental filtering and habitat characteristics, constraining species' ecological niche space, affect not only species composition, but also the structure of trophic interactions, resulting in large-scale variation in food-web structure along environmental gradients.

References

Arim, M. M. et al. 2007. On the relationship between trophic position, body mass and temperature: reformulating the energy limitation hypothesis. – Oikos 116: 1524–1530.

Aschan, M. M. et al. 2013. Change in fish community structure in the Barents Sea. – PLoS One 8: e62748.

Baiser, B. et al. 2012. Geographic variation in network structure of a nearctic aquatic food web. – Global Ecol. Biogeogr. 21: 579–591.

Bascompte, J. et al. 2005. Interaction strength combinations and the overfishing of a marine food web. – Proc. Natl Acad. Sci. USA 102: 5443–5447.

Blois, J. L. et al. 2013. Modeling the climatic drivers of spatial patterns in vegetation composition since the Last Glacial Maximum. – Ecography 36: 460–473.

Borrelli, J. J. and Ginzburg, L. R. 2014. Why there are so few trophic levels: selection against instability explains the pattern. – Food Webs 1: 10–17.

Boyce, D. G. et al. 2015a. From mice to elephants: overturning the 'one size fits all' paradigm in marine plankton food chains. – Ecol. Lett. 18: 504–515.

Boyce, D. G. et al. 2015b. Spatial patterns and predictors of trophic control across marine ecosystems. – Ecol. Lett. 18: 1001–1011.

Carmack, E. et al. 2015. Towards quantifying the increasing role of oceanic heat in sea ice loss in the new Arctic. – Bull. Am. Meteorol. Soc. 96: 2079–2105.

Certain, G. and Planque, B. 2015. Biodiversity baseline for large marine ecosystems: an example from the Barents Sea. – ICES J. Mar. Sci. 72: 1756–1768.

Cirtwill, A. R. et al. 2015. Latitudinal gradients in biotic niche breadth vary across ecosystem types. – Proc. R. Soc. B 282, 20151589.

Claessen, D. et al. 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. – Am. Nat. 155: 219–237.

Csardi, G. and Nepusz, T. 2006. The igraph software package for complex network research. – InterJournal Complex Syst. 1695: 1–9.

Cury, P. et al. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. – ICES J. Mar. Sci. 57: 603–618.

Dalpadado, P. et al. 2014. Productivity in the Barents Sea – response to recent climate variability. – PLoS One 9: e95273.

Degen, R. et al. 2016. Patterns and drivers of megabenthic secondary production on the Barents Sea shelf. – Mar. Ecol. Prog. Ser. 546: 1–16.

Dolgov, A. V. 2014. Feeding of non-target fish in the northern Barents Sea. – In: Karasev, A. B. (ed.), The formation of bioproductivity in the northern Barents Sea as response to warming in the Arctic. PINRO Press, pp. 155–185, in Russian.

Dolgov, A. V. et al. 2014. Feeding peculiarities of non-target fish and their role in productivity of the Kara Sea ecosystem. – VNIRO Proc. 152: 190–208, in Russian.

Duffy, J. E. et al. 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. – Nature 549: 261–264.

Dunne, J. A. 2009. Food webs. – In: Meyers, R. A. (ed.), Complex networks and graph theory section of the encyclopedia of complexity and systems science. Springer, pp. 3661–3682.

Dunne, J. A. et al. 2002. Food-web structure and network theory: the role of connectance and size. – Proc. Natl Acad. Sci. USA 99: 12917–12922.

Dunne, J. A. et al. 2004. Network structure and robustness of marine food webs. – Mar. Ecol. Prog. Ser. 273: 291–302.

Eklöf, A. et al. 2013. The dimensionality of ecological networks. – Ecol. Lett. 16: 577–583.

Eriksen, E. et al. 2016. The Barents Sea euphausiids: methodological aspects of monitoring and estimation of abundance and biomass. – ICES J. Mar. Sci. 73: 1533–1544.

Fossheim, M. et al. 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. – Nat. Clim. Change 5: 673–677.

Frainer, A. et al. 2017. Climate-driven changes in functional biogeography of Arctic marine fish communities. – Proc. Natl Acad. Sci. USA 114: 12202–12207.

France, R. L. 2012. Omnivory, vertical food-web structure and system productivity: stable isotope analysis of freshwater planktonic food webs. – Freshwater Biol. 57: 787–794.

Frank, T. K. et al. 2005. Trophic cascades in a formerly cod-dominated ecosystem. – Science 308: 1621–1623.

Gilarranz, L. J. et al. 2016. Anthropogenic effects are associated with a lower persistence of marine food webs. – Nat. Commun. 7: 10737.

Gillooly, J. F. et al. 2001. Effects of size and temperature on metabolic rate. – Science 293: 2248–2251.

Gislason, H. and Sinclair, M. M. 2000. Ecosystem effects of fishing. – ICES J. Mar. Sci. 57: 446–467.

Hansen, C. et al. 2016. Set-up of the Nordic and Barents Sea (NoBa) Atlantis model. – Technical Report IMR, Fisken og Havet nr. 2/2016, doi:10.13140/RG.2.1.3339.9929

Hattab, T. et al. 2016. Forecasting fine-scale changes in the food-web structure of coastal marine communities under climate change. – Ecography 39: 1227–1237.

Hop, H. and Gjøsæter, H. 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. – Mar. Biol. Res. 9: 878–894.

Ingvaldsen, R. et al. 2002. Variability in the Atlantic inflow to the Barents Sea based on a one-year time series from moored current meters. – Cont. Shelf Res. 22: 505–519.

Jennings, S. and Mackinson, S. 2003. Abundance–body mass relationships in size-structured food webs. – Ecol. Lett. 6: 971–974.

Johannesen, E. et al. 2012. Demersal fish assemblages and spatial diversity patterns in the Arctic-Atlantic transition zone in the Barents Sea. – PLoS One 7: e34924.

Johannesen, E. et al. 2016. Large-scale patterns in community structure of benthos and fish in the Barents Sea. – Polar Biol. 40: 237–246.

Jørgensen, L. L. et al. 2015. Distribution of benthic megafauna in the Barents Sea: baseline for an ecosystem approach to management. – ICES J. Mar. Sci. 72: 595–613.

Kaunzinger, C. M. K. and Morin, P. J. 1998. Productivity controls food-chain properties in microbial communities. – Nature 395: 495–497.

Kissling, W. D. and Schleuning, M. 2015. Multispecies interactions across trophic levels at macroscales: retrospective and future directions. – Ecography 38: 346–357.

Kortsch, S. et al. 2015. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. – Proc. R. Soc. B 282: 20151546.

Kortsch, S. et al. 2018. Data from: Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.k04q2kd>.

Legendre, P. and Legendre, L. 1998. Numerical ecology, 2nd ed. – Elsevier.

Lind, S. and Ingvaldsen, R. B. 2012. Variability and impacts of Atlantic Water entering the Barents Sea from the north. – Deep Sea Res. I 62: 70–88.

Lind, S. et al. 2016. Arctic layer salinity controls heat loss from deep Atlantic layer in seasonally ice-covered areas of the Barents Sea. – Geophys. Res. Lett. 43: 5233–5242.

Loeng, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. – Polar Res. 10: 5–18.

Loeng, H. and Drinkwater, K. 2007. An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. – Deep Sea Res. II 54: 2478–2500.

Loeuille, N. and M. Loreau. 2005. Evolutionary emergence of size-structured food webs. – Proc. Natl Acad. Sci. USA 102: 5761–5766.

MacArthur, R. H. and MacArthur, J. W. 1961. On bird species diversity. – Ecology 42: 594–598.

Marsh, J. M. et al. 2017. Ontogenetic, spatial and temporal variation in trophic level and diet of Chukchi Sea fishes. – Deep Sea Res. II 135: 78–94.

Maslanik, J. and Stroeve, J. 1999. Updated daily. Near-real-time DMSP SSM/I-SSMIS daily polar gridded sea-ice concentrations, 2008–2009. – National Snow and Ice Centre, Digital media, Boulder, CO, USA, 4-598.

May, R. M. 1973. Stability and complexity in model ecosystems. – Princeton Univ. Press.

McCann, K. and Hastings, A. 1997. Re-evaluating the omnivory–stability relationship in food webs. – Proc. R. Soc. B 264: 1249–1254.

Mecklenburg, C. W. et al. 2018. Marine fishes of the Arctic region, vol. 1. – CAFF Monitoring Series Report 28.

Meier, W. et al. 2006. Updated quarterly. Sea-ice concentrations from Nimbus-7 SMMR and DMSP SSM/I passive microwave data, 1978–2007. – National Snow and Ice Data Center, Digital media, Boulder, CO, USA.

Michalsen, K. et al. 2011. The joint Norwegian–Russian ecosystem survey: overview and lessons learned. – In: Proceedings of the 15th Russian–Norwegian Symposium 'Climate change and effects on the Barents Sea marine living resources', Longyearbyen, Norway, 6–9 September 2011, pp. 247–272.

Montoya, J. M. and Solé, R. V. 2002. Small world patterns in food webs. – J. Theor. Biol. 214: 405–412.

Morris, R. J. et al. 2015. Food web structure changes with elevation but not rainforest stratum. – Ecography 38: 792–802.

Neutel, A.-M. et al. 2007. Reconciling complexity with stability in naturally assembling food webs. – Nature 449: 599–602.

Newman, M. E. and Girvan, M. 2004. Finding and evaluating community structure in networks. – Phys. Rev. E 69: 026113.

O'Connor, M. I. et al. 2009. Warming and resource availability shift food web structure and metabolism. – PLoS Biol. 7: e1000178.

Oksanen, J. et al. 2007. Vegan: community ecology package. –<https://cran.r-project.org/package=vegan>.

Orlova, E. L. et al. 2013. Structure of the macroplankton–pelagic fish–cod trophic complex in a warmer Barents Sea. – Mar. Biol. Res. 9: 851–866.

Pecl, G. T. et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystem and human well-being. – Science 355: eaai9214.

Pellissier, L. et al. 2017. Comparing species interaction networks along environmental gradients. – Biol. Rev. doi:10.1111/brv.12366

Planque, B. 2016. Projecting the future state of marine ecosystems, "la grande illusion"? – ICES J. Mar. Sci. 73: 204–208.

Planque, B. et al. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? – ICES J. Mar. Sci. 79: 403–417.

Planque, B. et al. 2014. Who eats whom in the Barents Sea: a food web topology from plankton to whales. – Ecology 95: 1430–1430. Ecological Archives E095–124.

Poisot, T. et al. 2012. The dissimilarity of species interaction networks. – Ecol. Lett. 15: 1353–1361.

Poisot, T. et al. 2015. Beyond species: why ecological interaction networks vary through space and time. – Oikos 124: 243–251.

Polis, G. A. et al. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. – Annu. Rev. Ecol. Evol. Syst. 138: 297–330.

Reigstad, M. et al. 2011. Intra-regional comparison of productivity, carbon flux and ecosystem composition within the northern Barents Sea. – Prog. Oceanogr. 90: 33–46.

Riede, J. O. et al. 2010. Scaling of food-web properties with diversity and complexity across ecosystems. – Adv. Ecol. Res. 42: 139–170.

Romanuk, T. A. et al. 2005. The structure of food webs along river networks. – Ecography 29: 3–10.

Romanuk, T. A. et al. 2011. Trophic level scales with body size in fishes. – Global Ecol. Biogeogr. 22: 231–240.

Soberón, J. and Nakamura, M. 2009. Niches and distributional areas: concepts, methods, and assumptions. – Proc. Natl Acad. Sci. USA 106: 19644–19650.

Stouffer, D. B. and Bascompte, J. 2011. Compartmentalization increases food-web persistence. – Proc. Natl. Acad. Sci. USA. 108: 3648–3652.

Strona, G. et al. 2014. A fast and unbiased procedure to randomize ecological binary matrices with fixed row and column totals. – Nat. Commun. 5: 4114.

Suzuki, R. and Shimodaira, H. 2006. Pvclust: an R package for assessing the uncertainty in hierarchical clustering. – Bioinformatics 22: 1540–1542.

Tews, J. et al. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. – J. Biogeogr. 31: 79–92.

Thompson, R. M. and Townsend, C. R. 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. – Oikos 108: 137–148.

Thompson, R. M. et al. 2007. Trophic levels and trophic triangles: the prevalence of omnivory in real food web. – Ecology 88: 612–617.

Tilman, D. 1996. Population versus ecosystem stability. – Ecology 77: 350–363.

Tittensor, D. et al. 2010. Global patterns and predictors of marine biodiversity across taxa. – Nature 466: 1098.

Trøjelsgaard, K. et al. 2015. Geographical variation in mutualistic networks: similarity, turnover and partner fidelity. – Proc. R. Soc. B 282: 20142925.

Tylianakis, J. M. and Morris, R. M. 2017. Ecological networks across environmental gradients. – Annu. Rev. Ecol. Evol. Syst. 48: 25–48.

Vermaat, J. E. et al. 2009. Major dimensions in food-web structure properties. – Ecology 90: 278–282.

Ward, J. H. 1963. Hierarchical grouping to optimize an objective function. – J. Am. Stat. Assoc. 58: 263–244.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – Ecol. Monogr. 30: 279–338.

Wiedmann, M. A. et al. 2014. Life history variation in Barents Sea fish: implications for sensitivity to fishing in a changing environment. – Ecol. Evol. 4: 3596–3611.

Wood, S. A. et al. 2015. Effects of spatial scale of sampling on food web structure. – Ecol. Evol. 5: 3769–3782.

Wootton K. L. 2017. Omnivory and stability in freshwater habitats: does theory match reality? – Freshwater Biol. 62: 821–832.

Worm, B. and Myers, R. A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. – Ecology 84: 162–173.

Young, H. S. et al. 2013. The roles of productivity and ecosystem size in determining food chain length in tropical terrestrial ecosystems. – Ecology 94: 692–701.