

Paper 1

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Proceedings of the Royal Society B, 282, 20151546



Cite this article: Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M. 2015 Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proc. R. Soc. B* **282**: 20151546.
<http://dx.doi.org/10.1098/rspb.2015.1546>

Received: 30 June 2015

Accepted: 30 July 2015

Subject Areas:

ecology

Keywords:

biogeography, climate warming, fish community, modularity, network structure, food web topology

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2015.1546> or via <http://rspb.royalsocietypublishing.org>.

Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists

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Climate-driven poleward shifts, leading to changes in species composition and relative abundances, have been recently documented in the Arctic. Among the fastest moving species are boreal generalist fish which are expected to affect arctic marine food web structure and ecosystem functioning substantially. Here, we address structural changes at the food web level induced by poleward shifts via topological network analysis of highly resolved boreal and arctic food webs of the Barents Sea. We detected considerable differences in structural properties and link configuration between the boreal and the arctic food webs, the latter being more modular and less connected. We found that a main characteristic of the boreal fish moving poleward into the arctic region of the Barents Sea is high generalism, a property that increases connectance and reduces modularity in the arctic marine food web. Our results reveal that habitats form natural boundaries for food web modules, and that generalists play an important functional role in coupling pelagic and benthic modules. We posit that these habitat couplers have the potential to promote the transfer of energy and matter between habitats, but also the spread of perturbations, thereby changing arctic marine food web structure considerably with implications for ecosystem dynamics and functioning.

1. Introduction

Arctic marine ecosystems are exposed to rapid environmental change driven by accelerated warming [1,2]. Changes in habitat characteristics, such as reduced sea ice coverage and increased seawater temperature induce substantial food web reorganizations via regional gains and losses of species, potentially triggering cascading effects [3,4]. Temperature influences the distributions of marine organisms and recent poleward movements of boreal species have been documented as a response to warmer ocean temperatures and reduced sea ice coverage [5–7]. As a consequence, novel interactions will be established between incoming and resident species with implications for food web configuration and ecosystem functioning [8].

Food webs are structurally complex and contain a variety of sub-modules that may be treated as functional units [9–11]. Modularity refers to sub-groups of prey and predators interacting to a greater degree with each other than with species from other sub-groups, and is a food web property with implications for the dynamics and functioning of ecosystems [10]. According to network theory, food webs with greater modularity should be more persistent, as any perturbation effects may be retained within the modules, delaying or stopping their propagation to other modules [10,11]. Individual species can play different roles with respect to modularity, depending on how many feeding links they have within their own module and/or across modules [12].

From a network perspective, the ecological role of a species is a direct result of its position in the food web, the number of interactions it has with neighbouring species and their interactions, and also the strength of these interactions [13,14]. Some species are functionally more important than others and may have disproportionately large effects on food web structure [15]. Central and functionally unique species include keystone species, key species, ecosystem engineers and network hubs [16–18]. Theoretical and empirical results suggest that network hubs, or super-generalists, connect modules and communities due to their wide niche breadth, environmental tolerance, apex position in local communities and high motility [19–21]. If species affected by perturbations possess key functional roles in the food web, then the potential higher order, indirect effects of those perturbations on the entire food web structure can be dramatic.

A species' response to climate warming depends on several classes of traits, affecting its sensitivity and adaptability [22]. Among these traits, body size and feeding behaviour (e.g. generalist versus specialist) have particular relevance to food web structure. Large, migratory generalists are expected to respond rapidly to climate warming as they can easily move into new suitable regions, where they can exploit available niches and prey. Recent evidence shows that highly migratory, generalist fish are indeed moving poleward and entering arctic marine food webs [5,23–26]. To understand the implications of these poleward movements for ecosystem functioning and vulnerability, it is crucial to investigate how boreal taxa influence the structure of arctic marine food webs.

Network research offers a framework and the tools for characterizing the structure of food webs and the functional importance of species in ecosystems undergoing change [13]. Here, we use a network approach to explore and compare general structural properties of highly resolved boreal and arctic food webs of the Barents Sea. On the food web (network) level, we focus on structural properties with particular importance for food web dynamics such as the degree of modularity. On the species (node) level, we focus on taxa with central functional roles in the network. Further we evaluate potential changes in arctic marine food web structure due to poleward shifts of boreal species driven by climate warming. We ask the following questions: (i) what are the structural differences between boreal and arctic food webs of the Barents Sea? (ii) What roles do different taxa play with respect to modularity? (iii) How are the ongoing poleward shifts of boreal fish affecting the structure of arctic marine food webs?

2. Material and methods

(a) Study area and occurrence data

The Barents Sea is a large, open sub-arctic shelf sea bordering the Arctic Ocean (electronic supplementary material, figure S1). We defined a boreal and an arctic study region within the Barents Sea based on hydrology and species distributions (electronic supplementary material, figure S2a,b). We chose areas southwest and northeast of the polar front, the main hydrological demarcation separating boreal and arctic biogeographic regions of the Barents Sea (electronic supplementary material, figure S2a). Information on the occurrence of taxa within the defined study areas was obtained from data sampled by the joint Russian–Norwegian Ecosystem Survey in the Barents Sea. Since 2004, this survey has annually sampled plankton, fish and benthos at station

level, and sea birds and marine mammals along transects in August–September when sea ice extent is at its minimum [27].

Fish and epibenthos were allocated to the study regions based on station-wise (approx. 300 fish stations, approx. 40 epibenthos) presence/absence data. Occurrence of marine mammals, sea birds and zooplankton were assigned to specific sub-regions (see polygons in the electronic supplementary material, figure S2b) based on recordings from the Ecosystem Survey, and then assigned to the relevant study regions. All basal taxa were designated present in both regions, with the exception of sea ice algae, which are only included in the arctic marine food web. Results from the joint Russian–Norwegian Ecosystem Surveys can be found in several reports and research papers [5,27–29]. See the electronic supplementary material (appendix S1) for a more detailed description of the Barents Sea region, the boreal and the arctic study regions and the sub-sampling of taxa within these regions.

(b) The food webs

Food webs consist of trophospecies, i.e. groups of organisms (nodes) sharing the same predators and prey, and their feeding links [30]. In our food webs, individual trophospecies usually correspond to taxonomic species, but can sometimes refer to higher taxonomic groups, e.g. genus, family and class. The food web (meta-web) encompasses the most common taxa in the Barents Sea from the seafloor to the surface, comprising 233 trophospecies and 2192 feeding links. The food web includes detritus and bacteria, eight basal taxa, 43 zooplankton, 79 benthic and 77 fish trophospecies, as well as nine sea birds and 15 marine mammals. See the electronic supplementary material, tables S1 and S2, for exhaustive lists of all taxa included in the boreal and the arctic food webs, their degree (no. of trophic interactions), topological role, and habitat and functional group affiliation (e.g. basal taxa, zooplankton, benthos, fish, sea birds and marine mammals). Further details on how the food web was assembled and on the strength and limitations of the dataset are presented in the electronic supplementary material (appendix S1) and in Planque *et al.* [31]. The dataset files of the meta-web can be downloaded from the *Ecological archives* website [31].

The sub-webs specific for the boreal and the arctic regions were constructed by choosing subsets of taxa according to their occurrence (presence/absence) in the respective regions based on the Barents Sea Ecosystem Survey data (see further details in the electronic supplementary material, figure S2). The arctic marine food web is representative for the beginning of the recent warming period in the Barents Sea characterized by sea ice retraction and increasing water temperatures. The trophic interactions specific to the sub-regions were sub-sampled from the meta-web, assuming that species co-occurring in the sub-sampled regions and connected via trophic interactions in the meta-web, will also interact in the sub-webs. The two food webs differed with regard to trophospecies composition (127 unique and 106 shared trophospecies, see the electronic supplementary material, figure S3).

To evaluate the effect of the poleward movements of boreal fish on food web structure in the Arctic, we updated the arctic food web (hereafter referred to as arctic II) by including four fish species: atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), golden redfish (*Sebastes norvegicus*) and beaked redfish (*Sebastes mentella*). These fish were chosen because they have boreal affinities and display substantial responses to climate warming in terms of poleward shifts and biomass increases in the arctic region of the Barents Sea [5,23]. The trophic interactions between cod, haddock and the two redfish and other trophospecies in the arctic II food web were sub-sampled from the meta-web, assuming that trophospecies will interact in the sub-webs, if they interact in the meta-web. The boreal and the arctic Barents Sea food web files used in this study can be downloaded from the Dryad repository (doi:10.5061/dryad.73r6j).

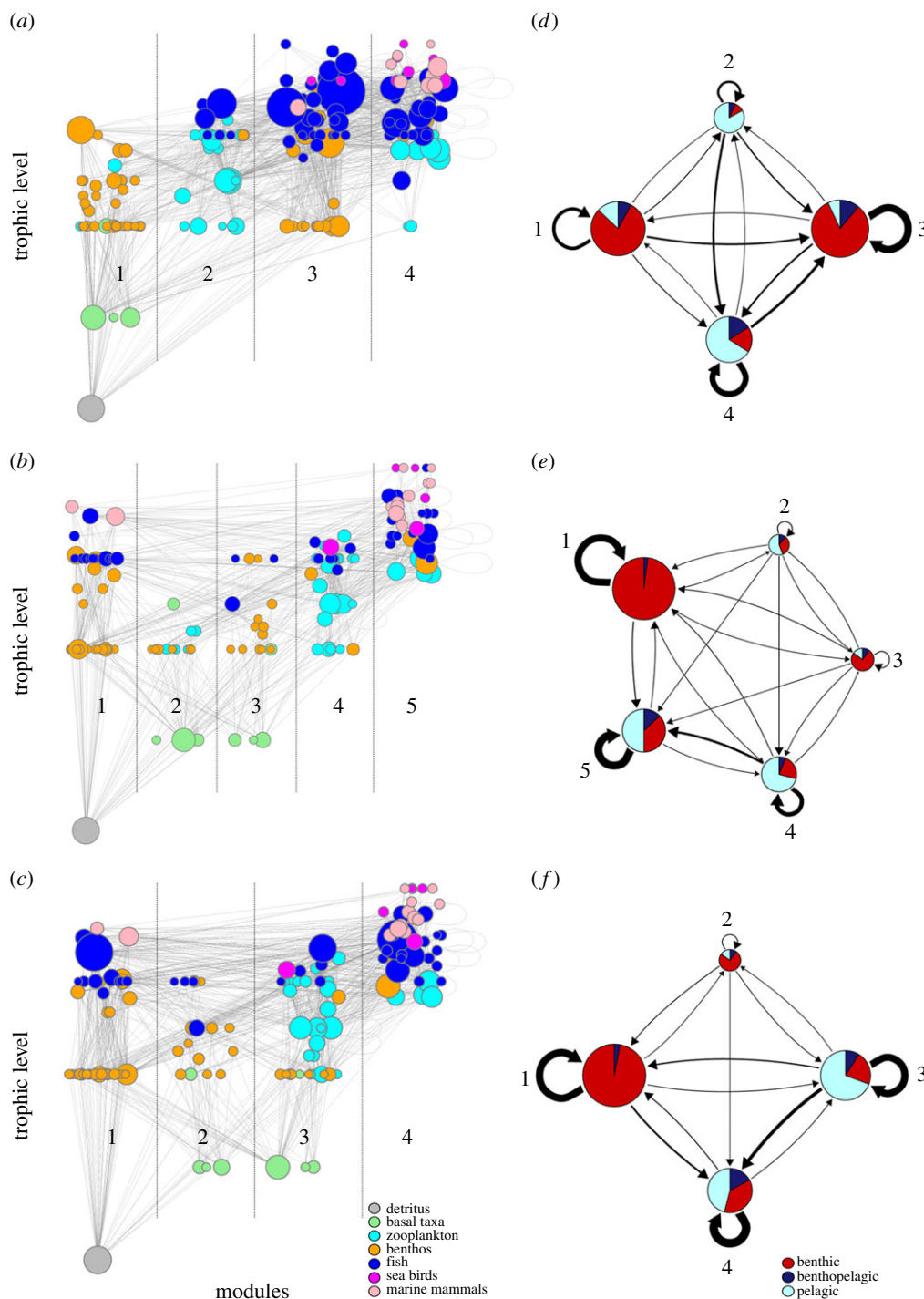


Figure 1. Food web diagrams of the Barents Sea for the (a) boreal, (b) arctic and (c) arctic II food webs. Each dot (node) represents a trophospecies. The lines connecting the nodes represent the feeding links between the trophospecies. The vertical position of the nodes indicates the trophic position of a species, and the horizontal position indicates the module affiliation of a species. The size of the nodes are proportional to the degree (no. of feeding links) of a species. The colour of the nodes indicates which functional group a trophospecies belongs to: grey, detritus; green, basal taxa; cyan, zooplankton; orange, benthos; blue, fish; magenta, sea birds; light pink, marine mammals. Schematic food web diagrams of the modular structure of the Barents Sea food webs: (d) boreal, (e) arctic and (f) arctic II food web. Each node (circle) represents a module in the corresponding food web. The size of the nodes indicates the number of trophospecies within each module. The colour of the nodes (pie charts) indicates the habitat affiliation of the trophospecies within the module: light blue, pelagic; red, benthic; dark blue, benthopelagic. The arrow width is proportional to the number of feeding links between modules in the direction of the arrowhead.

(c) Topological properties

To characterize the structure of our food webs, we estimated 12 food web metrics related to properties commonly addressed by topological food web analyses [32], including modularity (Mod). Number of species (S), number of trophic links (L), linkage density (LD, i.e. number of links per species) and connectance (C, i.e. the fraction of realized links). These are standard food web metrics that capture the fundamental complexity of food web structure. Other commonly

reported metrics include: percentage of trophospecies in loops, percentage of cannibals (self-loops), mean path length, mean clustering, mean omnivory and mean trophic level. The above metrics convey information about structural properties of food webs with implications for ecosystem dynamics and functioning [13,32]. See the electronic supplementary material, table S3, for abbreviations, short definitions of the food web metrics and their references. The number of loops was calculated using the software Network3D [33].

Table 1. Topological properties of boreal and arctic food webs of the Barents Sea. The arctic II food web contains four poleward moving fish: cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and two redfish species (*Sebastes norvegicus* and *Sebastes mentella*). The last two columns show the percentage difference for each food web metric between the boreal and the arctic (Diff B-A) food web and between the arctic II and the arctic (Diff All-A) food web.

metric	boreal	arctic	arctic II	Diff B-A (%)	Diff All-A (%)
number of species (S)	180	159	163	12	2
number of links (L)	1546	848	1078	45	21
linkage density (LD)	8.59	5.33	6.61	38	19
connectance (C)	0.05	0.03	0.04	40	25
%-Omni	52	41	43	21	5
%-Can	13	6	8	54	25
% in loops	13	0	3	—	—
meanPath	2.28	2.06	2.05	10	−1
meanOmni	0.40	0.33	0.34	18	3
meanSWTL	2.72	2.61	2.64	4	1
meanClust	0.25	0.17	0.21	32	19
modularity	0.27	0.35	0.30	−30	−17
modularity random ± s.d.	0.19 ± 0.003	0.25 ± 0.004	0.21 ± 0.003	—	—

(d) Degree distributions

The degree of a trophospecies refers to its total number of feeding links with other species and is used as a measure of food web centrality (i.e. degree centrality). Species with many connections, i.e. high degree and central species (hubs), tend to have a large impact on overall food web structure and functioning [34]. In a directed network such as a food web, the degree of a trophospecies can be decomposed into its in-degree and out-degree. In-degree refers to the number of links directed towards a trophospecies, which is the total number of its prey (i.e. its generality). The out-degree is the number of outgoing links, which is the total number of predators of a trophospecies (i.e. its vulnerability). The cumulative out- and in-degree distributions were calculated to compare the generality and the vulnerability of the trophospecies among the food webs.

To investigate how the average degree centrality has changed in the Arctic due to the poleward movement of boreal, generalist fish, we mapped the mean degree centrality at station level for the years 2004 (491 stations) and 2012 (377 stations) based on 51 fish taxa. The year 2004 is representative of the species composition and food web structure in the arctic Barents Sea in the early stage of warming experienced during the last decade [5]. The station-wise mean degree centrality calculations of fish were based on the degrees of fish in the Barents Sea meta-web. To help visualize and compare the spatial patterns, we interpolated the mean degree on a regular grid by universal kriging [35], and colour-coded the results in the Barents Sea maps. The size of the grid was 50 × 50 km (approx. 27 nautical miles) to ensure at least one station per grid cell. See the electronic supplementary material, figure S4 for annual degree centrality maps between 2004 and 2012, and electronic supplementary material, table S4 for a list of the 51 fish taxa included in the analysis.

(e) Modularity analysis

For each food web, we calculated modularity, describing how densely sub-groups of species interact with one another compared to species from other sub-groups [36]. To find the best partition, we used the simulated annealing algorithm proposed by Reichardt & Bornholdt [37], a stochastic optimization approach that identifies modules by maximizing a modularity

function [12]. For a given partition of a food web, the index of modularity M is defined as:

$$M = \sum_{s=1}^{N_M} \left(\frac{I_s}{L} - \left(\frac{d_s}{2L} \right)^2 \right),$$

where N_M is the number of modules s , I is the number of links between nodes in module s , L is the number of links in the network and d_s is the sum of degrees of all species in module s . The modularity value M lies in the interval $[0, 1]$ and for a random partition M equals 0. To test whether our empirical networks were significantly more modular than random networks, we compared the modularity of our empirical networks with the modularity of 1000 randomized networks constrained by the same species degree distribution as the empirical network. To address whether the modules were associated with habitat use (pelagic or benthic) and short-weighted trophic level of component trophospecies [38], we applied linear discriminant analyses (LDA) [21]. The habitat affiliation of each trophospecies was coded B (benthic), P (pelagic) and BP (benthopelagic). Each LDA was followed by a permutation test to assess the significance of the association.

(f) Topological roles of the species

We estimated the topological role of each species based on their module membership. We relied on module membership identified by a randomly chosen replicate of the simulated annealing algorithm. The role is described by two parameters: (i) the standardized within-module degree z and (ii) the among-module connectivity participation coefficient PC. The z -score reflects how well a species is connected to other species inside the module relative to other species within its own module. The PC parameter estimates the distribution of a species' connections across the modules. The z -score is defined as

$$z = \frac{k_{is} - \bar{k}_s}{SD_{k_s}},$$

where k_{is} is the number of links from species i to other species in its own module s and \bar{k}_s and SD_{k_s} are the average and standard deviation of k_{is} over all species in s . The role of a species can also be described by its links to species in modules other than its own. The among-module connectivity PC can be defined as the

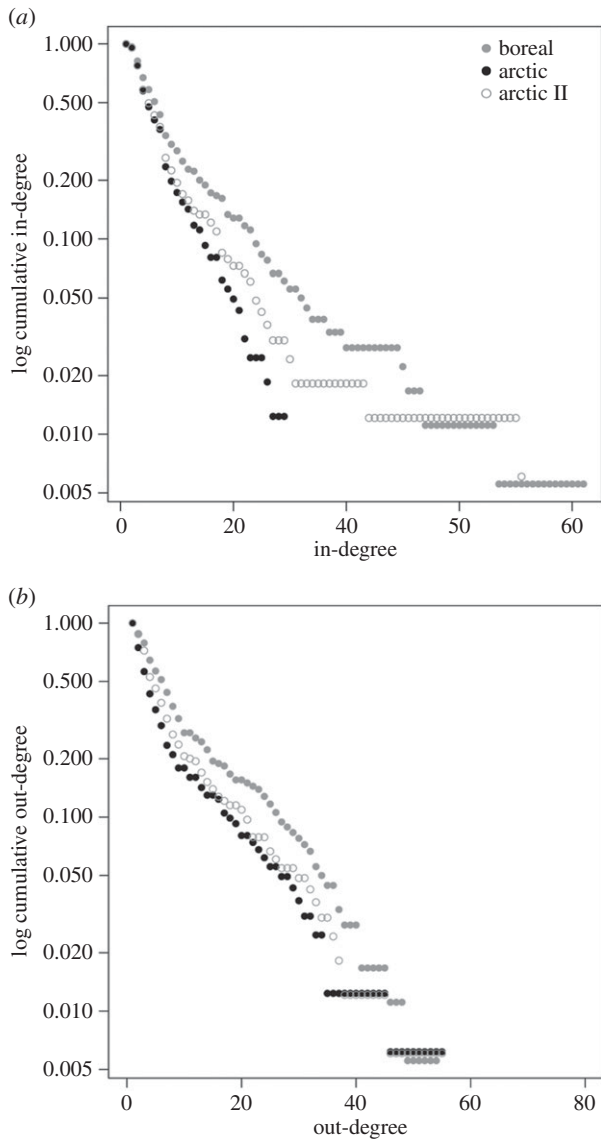


Figure 2. Cumulative (a) in- and (b) out-degree distributions of the boreal (grey circles), arctic (black circles) and arctic II (open circles) food webs. The in-degree represent the number of prey items of a species, i.e. its generality. The out-degree represent the number of predators of a species, i.e. its vulnerability.

number of links from species i to species in other modules, normalized by the degree (k_i) of species i :

$$PC = 1 - \sum_{t=1}^{N_M} \left(\frac{k_{it}}{k_i} \right)^2,$$

where k_i is the number of links to or from species i and k_{it} is the number of links from species i to species in module t . Owing to the stochastic nature of the module detection algorithm, we estimated and plotted the mean and 95% CI of the 1000 within-module (z) and 1000 among-module (PC) role affiliations.

The z -PC parameter space is divided into four regions modified from Guimera *et al.* [12]. The thresholds that define the topological roles are $z = 2.5$ and $PC = 0.625$. If a species has at least 60% of its links within its own module then $PC < 0.625$. If a species has $z \geq 2.5$ and $PC < 0.625$, it is classified as a module hub, having many links within its own module. Species that are in the region $z < 2.5$ and $PC < 0.625$ are called peripherals or specialists. These are species that have relatively few links and most of their links are within their own module. Species that are in the region $z < 2.5$ and $PC \geq 0.625$ are module connectors. Species in the region $z \geq 2.5$ and $PC \geq 0.625$ are hub network connectors. These species are

characterized by high within- and between-module connectivity and are classified super-generalists.

All data analyses were performed in the statistical software R v. 3.1.0. The degree distributions and modularity were calculated using the R package ‘igraph’. The kriging of the degree centrality of fish was performed using the R package ‘gstat’, and the permutation tests associated with the LDAs were calculated using the R package ‘vegan’.

3. Results

(a) Topological properties

The Barents Sea food webs differed with regard to structural properties and modularity (figure 1). Number of trophospecies was somewhat higher in the boreal (180) compared to the arctic marine food web (159), partly due to the higher fish species richness in this region (electronic supplementary material, figure S3a). The boreal food web with its 1546 links had nearly double as many feeding links as the arctic food web with its 848 links (table 1). Complexity measures such as links per species and connectance were, respectively, 38% and 40% higher in the boreal food web (table 1). The boreal food web also had higher clustering (32%) and more cannibals (54%), and contained many loops (13%), whereas the arctic food web contained no loops. We re-analysed the arctic food web after including four boreal poleward moving fish (cod, haddock, golden redfish and beaked redfish) to evaluate their effect on the arctic food web structure. The inclusion of these fish species resulted in the structural descriptors of the arctic food web becoming more similar to the boreal food web (table 1). Modularity decreased by 17%, whereas connectance, linkage density, clustering and number of cannibals increased by 25%, 19%, 19% and 25%, respectively. The arctic II marine food web also contained 3% species in loops.

(b) Degree distributions and degree centrality maps

We analysed the in- (number of prey) and out- (number of predators) degree distributions of the food webs (figure 2). The cumulative log-linear plots indicate that in- and out-degree for both regions follow an exponential degree distribution. The boreal food web in-degree distribution was less steep than the arctic, indicating that the boreal food web contained a greater number of trophic generalists. The three trophospecies with the highest degree in the boreal food web were: cod (112 links), haddock (88 links) and beaked redfish (62 links). The three trophospecies with the highest degree in the arctic food web, apart from detritus, were phytoplankton (44 links), polar cod (*Boreogadus saida*, 42 links) and northern shrimp (*Pandalus borealis*, 41 links).

After including cod, haddock and the two redfish to the arctic food web, the in-degree distribution of the arctic II food web became less steep. The spatial mappings of the mean degree centrality of fish in the Barents Sea showed clear differences in 2004 between the boreal region characterized by a high mean degree of fish, and the arctic region characterized by a low mean degree of fish. By 2012, this gradient had weakened throughout the whole Barents Sea due to a strong increase in the mean degree in the Arctic (figure 3). The annual (2004–2012) degree centrality maps illustrate how the mean degree centrality of fish in the Arctic increased during the recent period of warming in the Barents Sea (electronic supplementary material, figure S4).

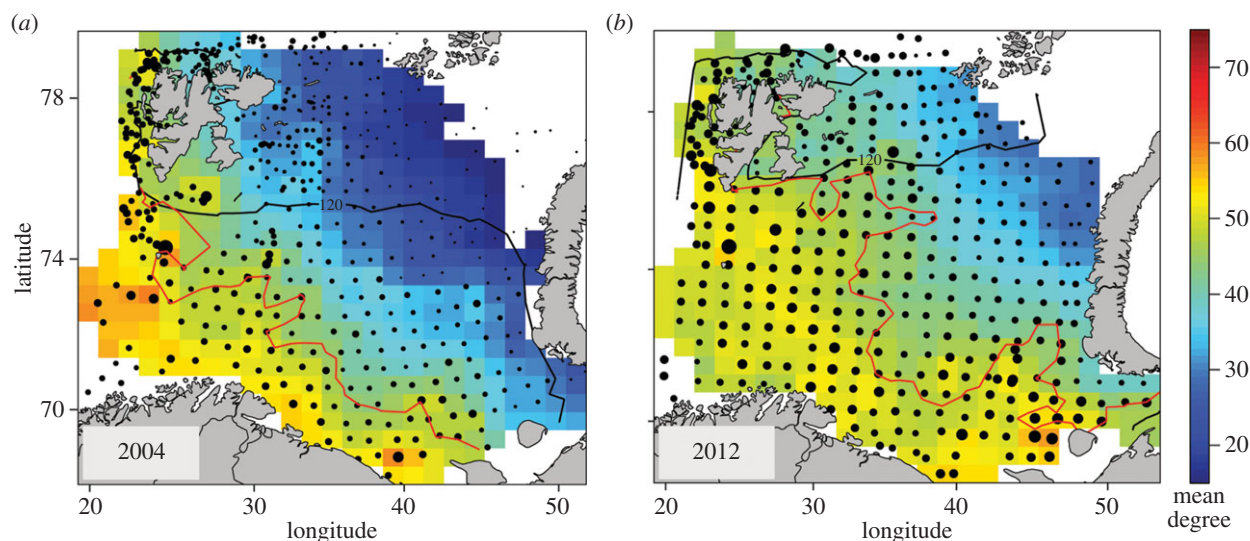


Figure 3. Barents Sea maps of mean degree centrality (mean no. of feeding links) of 51 fish for the years (a) 2004 and (b) 2012. The dots indicate the position of sampling stations (approx. 400) and the size of the dots is proportional to the mean fish degree at the station. The coloured surface (colour code shown in the legend) indicates the mean degrees of fish, spatially interpolated on a regular grid. North of the 120 day isolines (black lines) sea ice was present for more than 120 days during the year. The red lines indicate the 2°C isotherm, southwest of the isotherm seawater temperatures are more than 2°C (atlantic water) and northeast of the isotherm the temperatures are less than 2°C (mixed water and arctic water). See the electronic supplementary material, figure S2 for the position of the boreal and arctic study regions in the Barents Sea.

(c) Modularity and the topological role of species

The modularity analysis divided the boreal food web into four distinct modules, the arctic food web into five and the arctic II food web into four (figure 1). The structure of all empirical food webs was significantly ($p < 0.01$) more modular than that of networks with the same degree distributions but random interaction between species (table 1). Modularity was 30% higher in the arctic food web (0.35) than in the boreal (0.27) (table 1). The LDAs significantly discriminated modules by trophic levels and habitat use (boreal $p < 0.001$, and arctic $p < 0.001$), indicating that some modules are dominated by benthic trophospecies and others by pelagic (electronic supplementary material, figure S5). Modules were also separated across trophic levels (electronic supplementary material, figure S5).

Topological role analysis showed that, when present, cod and haddock are hub network connectors, playing a high within as well as between-module connecting role (figure 4*a,c*). These two fish are characterized by a high in-degree (many prey) and thus function as super-generalists in the food web. When present in the arctic food web, cod, haddock and beaked redfish (also a module connector) tie modules together, thereby reducing the modularity (table 1 and electronic supplementary material, figure S6). As cod and haddock are the only super-generalists in the food webs and display the most pronounced effect on food web structure, much of the discussion will focus on their food web structuring role. Exhaustive lists of all species and their role as peripherals, connectors, module connectors or network connectors can be found in the electronic supplementary material, tables S1 and S2.

4. Discussion and conclusion

(a) Topological properties of the boreal and the arctic marine food webs

Comparison of food web properties revealed considerable differences in structure and link configuration between the boreal and the arctic food webs in the Barents Sea, despite

similar number of taxa in each functional group (i.e. groups such as benthos and fish). The boreal food web displayed higher diversity of trophospecies, mainly due to higher fish species richness, and considerably more links, more cannibals, higher clustering and more trophospecies in loops. The greater number of feeding links in the boreal food web is due to more generalists at higher trophic levels. The presence of relatively many species in loops in the boreal food web may be attributed to higher mutual predation and higher levels of omnivory, whereas higher clustering may be attributed to a greater incidence of within-chain omnivory [39].

The two food webs also displayed similarities, e.g. they had similar mean path lengths and mean trophic levels. The high number of omnivores and cannibals seems to be an inherent feature of marine systems when compared to non-marine systems [32], probably because many fish commonly use these feeding strategies [40]. The food webs had short path length (two degrees of separation); a seemingly universal property of food webs, indicating that species are close neighbours [41,42]. This implies that environmental perturbations, e.g. from climate warming or overfishing, can spread rapidly through the food web, affecting many species indirectly. Such indirect, higher-order effects of environmental perturbations, i.e. effects mediated via a third species by predation or competition, may have greater impact on food web configuration than direct effects [43]. Recent studies from arctic terrestrial and marine systems show how climate-driven effects on community structure are often indirect and mediated via predation or facilitation [4,44].

(b) Degree distributions and degree centrality maps

The estimated degree distributions follow an exponential distribution, which supports previous studies of food webs with mid-range (0.03–0.05) connectance [41]. However, the in-degree (no. of prey) distribution was steeper for the arctic food web, suggesting that, on average, arctic trophospecies have narrower niches than boreal trophospecies. The arctic marine food web is known to contain many specialized

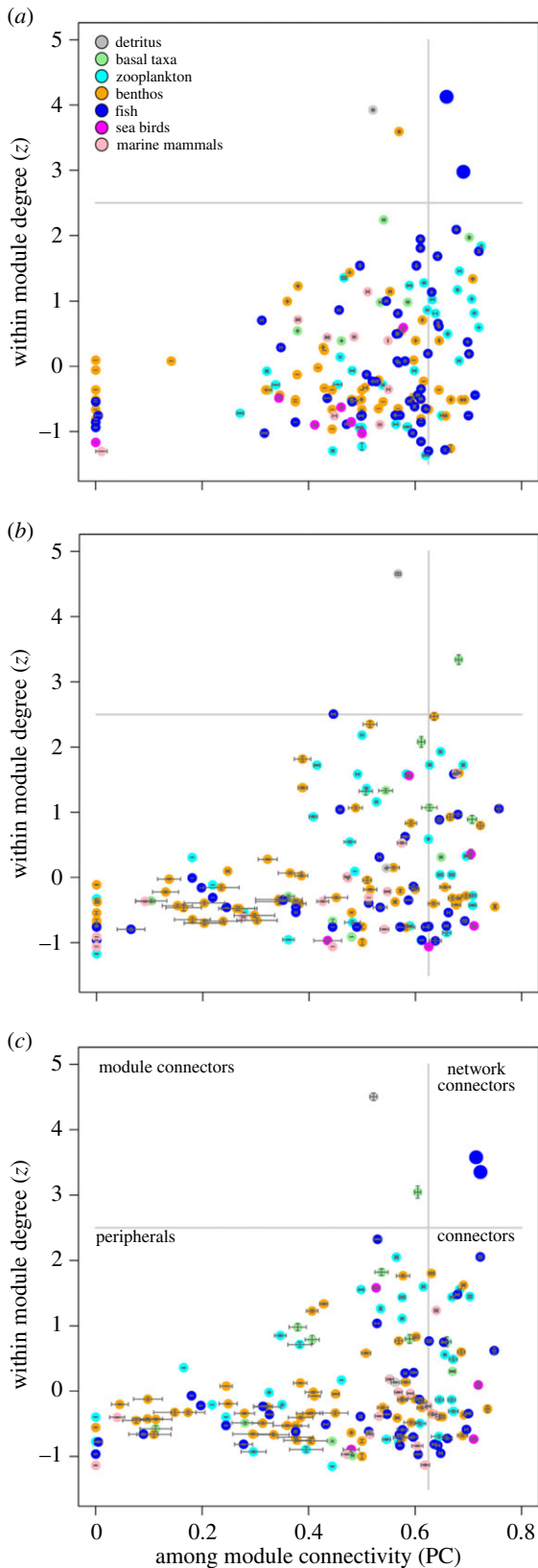


Figure 4. Species topological roles with respect to modularity: (a) boreal, (b) arctic (c) and arctic II food webs. Dots are mean values based on 1000 estimates, and the error bars indicate the 95% CIs for z and PC. The topological network roles are: network connectors (upper right), module connectors (upper left), peripherals (lower left) and connectors (lower right). The colours, top left legend in (a), correspond to the functional affiliation of a trophospecies: grey, detritus; green, basal taxa; cyan, zooplankton; orange, benthos; blue, fish; magenta, sea birds; light pink, marine mammals. The larger blue dots in (a) and (c), upper right quadrant, are the two network connector hubs, cod and haddock. See the electronic supplementary material (tables S1 and S2) for lists of all taxa and their topological role.

benthivore fish (e.g. *Liparis* spp.) [5], but also many sympagic specialists (e.g. polar cod and the crustacean *Gammarus wilkitzkii*) which live in close association with the sea ice habitat. On the other hand, the boreal marine region of the Barents Sea is characterized by many large generalists as documented in this study (e.g. cod, haddock, wolffishes *Anarhichas* spp., redfishes, etc.).

The mean degree centrality maps show that fish in the southern Barents Sea have, on average, a higher degree. In 2004, the contrast between the mean degree in the boreal and the arctic region was sharp, but by 2012 this difference had weakened because of the increased mean degree of fish in the Arctic. The extensive spatial changes in the mean degree of fish in the period 2004–2012 (illustrated by our degree centrality maps) highlight the rapid structural changes taking place in the arctic Barents Sea due to the poleward shifts of boreal generalists. The recent increase of boreal fish generalists in the Arctic can be explained by their ability to take advantage of a diverse range of prey and adjust to a varying and unpredictable environment as experienced in a warming Arctic [45]. A property such as generalism directly affects the interaction structure of species and may have many indirect high-order effects on food web structure (e.g. by connecting energetic pathways and changing interaction parameters between species). The increase of fish diversity and abundances at higher trophic levels in the arctic region of the Barents Sea could enhance top-down regulation of the arctic marine food web [5,29].

(c) Modularity and topological roles of trophospecies

One of the food web properties that is strongly affected by highly connected generalists is modularity. The importance of highly connected nodes, network hubs, for modularity has been stressed previously in a variety of biological systems, including genetic [46], metabolic [12], spatial [19,47,48], mutualistic [49,50] and food web networks [21]. We show that, in the Arctic, inclusion of the boreal super-generalists leads to a decrease in modularity. The extent of this decrease depends on the nature of the modules and on how the species' links are distributed within and among modules, i.e. a species' topological role. In this study, food web modules are significantly associated with habitats (benthic and pelagic) and trophic levels, stressing that habitats form natural boundaries for marine food web modules, a result consistent with previous findings from a Caribbean marine ecosystem [21].

Given that modules are separated by habitats, habitat generalists like cod will forage across modules, linking modules and reducing overall modularity. Two of the poleward moving species, cod and haddock, have the widest ecological niches in our study, being generalists and omnivores. By feeding across many trophic levels and across pelagic and benthic habitats, these species have a particularly strong effect on modularity. The increased coupling of benthic and pelagic habitats by these fish will potentially lead to changes in ecosystem functioning in the Arctic. We hypothesize that energetic pathways across modules will increase, promoting the transfer of matter and energy from one module to another, as well as the spread and effects of perturbations.

From another well-studied marine region (Nova Scotia) in the northwest Atlantic, we know that the sudden disappearance of cod has led to the reorganization of the food web [51]. The removal of cod was followed by an increase in benthic

crustaceans such as northern shrimp and snow crab (*Chionoecetes opilio*). Northern shrimp and the invasive snow crab are present in the northeast Barents Sea food web, where they play a module connecting role. We conjecture here that the abrupt structural shift induced by cod in Nova Scotia may be attributed to cod's role as a food web network connector hub. The take-over by northern shrimp and snow crab could indicate that the loss of an important network connector may be substituted by increasing abundances of other module connecting species, performing similar module connecting roles, but changing community structure fundamentally due to distinct trophic network positions.

Species with fewer interactions may also have large structural impact depending on their network position (and on the strength of their interactions) [14,18]. Our topological role analysis shows that a few species (approx. 20%) are structurally very important. These trophospecies connect modules, but not the entire network. Module connectors in the Barents Sea food webs are key species occupying high trophic levels such as beaked redfish, polar cod, wolffishes, snow crab, fulmar (*Fulmarus glacialis*), ringed and bearded seal (*Phoca hispida* and *Erignathus barbatus*), but also low trophic level species such as northern shrimp, northern krill (*Meganctiphanes norvegica*) and calanoid copepods (*Calanus* spp.). Interestingly, several taxa with few trophic interactions (low degree) possess module connecting roles due to their position in the network, e.g. the eelpout (*Lycodes gracilis*) and the sculpin species (*Triglops* spp. and *Icelus* spp.). Populations of sculpins (*Icelus* spp.) have been declining recently in the arctic region of the Barents Sea, which is remarkable considering that the arctic region has become more productive [5,28]. A potential explanation for the recent local decline of these structurally important arctic fish species are predation and competition by the increasingly abundant boreal fish generalists [5].

(d) Observed and expected changes in arctic marine food web structure

Increasing seawater temperatures, reduced sea ice coverage and longer duration of the ice-free periods will open 'thermal' windows of opportunity for expanding boreal species and novel communities in the Arctic [28]. Fish, in particular, but also sea birds are among the quickest to respond to climate warming due to their high motility. In the northern Barents Sea, boreal sea birds (e.g. *Alca torda*, *Fratercula arctica* and *Uria aalge*) are increasing in abundance [52]. These migratory top predators move into suitable habitats in the search for prey, and indeed, in the arctic region of the Barents Sea, they find a pelagic community increasingly dominated by atlantic zooplankton such as *Calanus finmarchicus*, krill and capelin [52]. We hypothesize that the increase in boreal prey availability may favour boreal top predators in the resource competition with arctic top predators.

The observed changes in arctic community structure alter interaction parameters, particularly between taxa at higher trophic levels [53]. While many boreal taxa have become more abundant in the northern Barents Sea, some arctic taxa have been declining. For example, abundances of the arctic sea birds, Brünnichs guillemot (*Uria lomvia*) and possibly little auk (*Alle alle*) are declining, as is the case for some arctic pelagic (e.g. polar cod) and benthivore fish (e.g. *Liparis* spp.) [5,52]. Marine mammals (the harp seal *Phagophilus groenlandicus* and the minke whale *Balenoptera acutorostrata*) also seem to be affected by the presence of boreal fish competitors (e.g. cod) as indicated by observed declines in their body condition [53]. Although it is notoriously hard to predict the outcome of species interactions, the effects of alterations in energetic pathways within and between pelagic and benthic compartments of the arctic food web will have far-reaching ramifications for dynamics and functioning, permeating through the entire food web network.

5. Concluding remarks

Some of the most prompt responses to climate warming are altered migration patterns of opportunistic, generalist fish. The poleward expansion of these fish generalists alters the structure of arctic food webs, increasing the connectivity between benthic and pelagic habitat modules while reducing the modularity. Establishing and reinforcing energetic pathways between food web compartments will affect ecosystem functioning. We expect that in a more densely connected and less modular arctic marine food web, species will be closer neighbours, resulting in matter, energy, but also the effects of perturbations, spreading further and faster across the ecosystem.

Data accessibility. The food web data used in this study can be downloaded from the Dryad repository: <http://dx.doi.org/10.5061/dryad.73r6j>.

Authors' contributions. S.K. and R.P. conceived and designed the study, analysed the data and interpreted the results; R.P. coordinated the study; S.K., R.P., A.D. and M.A. discussed the concepts; S.K. compiled the food web data assisted by A.D. and M.A.; M.F. compiled the fish data; S.K. wrote the manuscript in collaboration with R.P. and with inputs from M.F., A.D. and M.A. All authors gave their final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. We gratefully acknowledge the support of the Norwegian Research Council for funding of the *BarEcoRe* project (200793/S30). S.K. acknowledges the support of the Troms Science Foundation

Acknowledgements. The authors would like to thank the Marine Research Institute (IMR, Norway) and Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia) for their joint efforts in generating the Barents Sea ecosystem data used in this study. We acknowledge all who have contributed to construct and improve the Barents Sea food web database. Also thanks to the participants who helped to construct the polygon-wise species distribution of the Barents Sea during the spatial *BarEcoRe* (Barents Sea ecosystem resilience under global environmental change) workshop held in Tromsø in 2012. Thanks also to Jian D. L. Yen for reviewing a previous draft of the manuscript.

References

- Overland JE, Wang M. 2013 When will the summer Arctic be nearly sea ice free? *Geophys. Res. Lett.* **40**, 2097–2101. (doi:10.1002/grl.50316)
- Hoegh-Guldberg O, Bruno JF. 2010 The impact of climate change on the world's marine ecosystems. *Science* **328**, 1523–1528. (doi:10.1126/science.1189930)
- Albouy C, Velez L, Coll M, Colloca F, Loc'h FL, Mouillot D, Gravel D. 2014 From projected species distribution to food-web structure under climate change. *Glob. Change Biol.* **20**, 730–741. (doi: 10.1111/gcb.12467)

4. Kortsch S, Primicerio R, Beuchel F, Renaud PE, Rodrigues J, Lønne OJ, Gulliksen B. 2012 Climate-driven regime shifts in Arctic marine benthos. *Proc. Natl. Acad. Sci. USA* **109**, 14 052–14 057. (doi:10.1073/pnas.1207509109)
5. Fossum M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV. 2015 Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat. Clim. Change* **5**, 673–677. (doi:10.1038/nclimate2647)
6. Cheung WW, Watson R, Pauly D. 2013 Signature of ocean warming in global fisheries catch. *Nature* **497**, 365–368. (doi:10.1038/nature12156)
7. Poloczanska ES *et al.* 2013 Global imprint of climate change on marine life. *Nat. Clim. Change* **3**, 919–925. (doi:10.1038/nclimate1958)
8. Beaupre G, Edwards M, Raybaud V, Goberville E, Kirkyby RR. 2015 Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nat. Clim. Change* **5**, 695–701. (doi:10.1038/nclimate2650)
9. Milo R, Shen-Orr S, Itzkovitz S, Kashtan N, Chklovskii D, Alon U. 2002 Network motifs: simple building blocks of complex networks. *Science* **298**, 824–827. (doi:10.1126/science.298.5594.824)
10. Stouffer DB, Bascompte J. 2011 Compartmentalization increases food-web persistence. *Proc. Natl. Acad. Sci. USA* **108**, 3648–3652. (doi: 10.1073/pnas.1014353108)
11. Krause AE, Frank KA, Mason DM, Ulanowicz RE, Taylor WW. 2003 Compartments revealed in food-web structure. *Nature* **426**, 282–285. (doi:10.1038/nature02115)
12. Guimera R, Amaral LAN. 2005 Functional cartography of complex metabolic networks. *Nature* **433**, 895–900. (doi:10.1038/nature03288)
13. Dunne JA. 2006 The network structure of food webs. In *Ecological networks. Linking structure to dynamics in food web* (eds M Pascual, J Dunne), pp. 27–86. New York, NY: Oxford University Press.
14. Berlow EL. 1999 Strong effects of weak interactions in ecological communities. *Nature* **398**, 330–334. (doi:10.1038/18672)
15. Aufderheide H, Rudolf L, Gross T, Lafferty KD. 2013 How to predict community responses to perturbations in the face of imperfect knowledge and network complexity. *Proc. R. Soc. B* **280**, 20132355. (doi:10.1098/rspb.2013.2355)
16. Jordán F, Scheuring I. 2002 Searching for keystones in ecological networks. *Oikos* **99**, 607–612. (doi:10.1034/j.1600-0706.2002.11889.x)
17. Jones CG, Lawton JH, Shachak M. 1996 Organisms as ecosystem engineers. In *Ecosystem management*, pp. 130–147. New York, NY: Springer.
18. Paine RT. 1969 A note on trophic complexity and community stability. *Am. Nat.* **929**, 91–93. (doi:10.1086/282586)
19. Borthagaray AI, Arim M, Marquet PA. 2014 Inferring species roles in metacommunity structure from species co-occurrence networks. *Proc. R. Soc. B* **281**, 20141425. (doi:10.1098/rspb.2014.1425)
20. Guimera R, Stouffer D, Sales-Pardo M, Leicht E, Newman M, Amaral L. 2010 Origin of compartmentalization in food webs. *Ecology* **91**, 2941–2951. (doi: 10.1890/09-1175.1)
21. Rezende EL, Albert EM, Fortuna MA, Bascompte J. 2009 Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecol. Lett.* **12**, 779–788. (doi:10.1111/j.1461-0248.2009.01327.x)
22. Rijnsdorp AD, Peck MA, Engelhard GH, Möllmann C, Pinnegar JK. 2009 Resolving the effect of climate change on fish populations. *ICES J. Mar. Sci.* **66**, 1570–1583. (doi:10.1093/icesjms/fsp056)
23. Mueter FJ, Litzow MA. 2008 Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecol. Appl.* **18**, 309–320. (doi:10.1890/07-0564.1)
24. Hollowed AB, Sundby S. 2014 Change is coming to the northern oceans. *Science* **344**, 1084–1085. (doi:10.1126/science.1251166)
25. Kjesbu OS, Bogstad B, Devine JA, Gjøsæter H, Howell D, Ingvaldsen RB, Nash RD, Skjæraasen JE. 2014 Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proc. Natl. Acad. Sci. USA* **111**, 3478–3483. (doi:10.1073/pnas.1316342111)
26. Hollowed A *et al.* 2013 Projected impacts of climate on marine fish and fisheries. *ICES J. Mar. Sci.* **70**, 1023–1073. (doi:10.1093/icesjms/fst081)
27. Michalsen K *et al.* 2013 Marine living resources of the Barents Sea—ecosystem understanding and monitoring in a climate change perspective. *Mar. Biol.* **9**, 932–947. (doi:10.1080/17451000.2013.775459)
28. Dalpadado P *et al.* 2014 Productivity in the Barents Sea—response to recent climate variability. *PLoS ONE* **9**, e95273. (doi:10.1371/journal.pone.0095273)
29. Wiedmann MA, Aschan M, Certain G, Dolgov A, Greenacre M, Johannesen E, Planque B, Primicerio R. 2014 Functional diversity of the Barents Sea fish community. *Mar. Ecol. Prog. Ser.* **495**, 205–218. (doi:10.3354/meps10558)
30. Yodzis P, Winemiller KO. 1999 In search of operational trophospecies in a tropical aquatic food web. *Oikos* **87**, 327–340. (doi:10.2307/3546748)
31. Planque B *et al.* 2014 Who eats whom in the Barents Sea: a food web topology from plankton to whales: ecological Archives E095–124. *Ecology* **95**, 1430–1430. (doi:10.1890/13-1062.1)
32. Dunne JA, Williams RJ, Martinez ND. 2004 Network structure and robustness of marine food webs. *Mar. Ecol. Prog. Ser.* **273**, 291–302. (doi:10.3354/meps273291)
33. Williams R. 2010 *Network 3D software*. Cambridge, UK: Microsoft Research.
34. Strogatz SH. 2001 Exploring complex networks. *Nature* **410**, 268–276. (doi:10.1038/35065725)
35. Pebesma EJ. 2004 Multivariable geostatistics in S: the gstat package. *Comput. Geosci.* **30**, 683–691. (doi:10.1016/j.cageo.2004.03.012)
36. Newman ME, Girvan M. 2004 Finding and evaluating community structure in networks. *Phys. Rev. E* **69**, 026113. (doi:10.1103/PhysRevE.69.026113)
37. Reichardt J, Bornholdt S. 2006 Statistical mechanics of community detection. *Phys. Rev. E* **74**, 016110. (doi:10.1103/PhysRevE.74.016110)
38. Williams RJ, Martinez ND. 2004 Limits to trophic levels and omnivory in complex food webs: theory and data. *Am. Nat.* **163**, 458–468. (doi:10.1086/381964)
39. Ings TC *et al.* 2009 Review: ecological networks—beyond food webs. *J. Anim. Ecol.* **78**, 253–269. (doi:10.1111/j.1365-2656.2008.01460.x)
40. Thompson RM, Hemberg M, Starzomski BM, Shurin JB. 2007 Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology* **88**, 612–617. (doi:10.1890/05-1454)
41. Dunne JA, Williams RJ, Martinez ND. 2002 Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci. USA* **99**, 12 917–12 922. (doi:10.1073/pnas.192407699)
42. Williams RJ, Berlow EL, Dunne JA, Barabási A-L, Martinez ND. 2002 Two degrees of separation in complex food webs. *Proc. Natl. Acad. Sci. USA* **99**, 12 913–12 916. (doi:10.1073/pnas.192448799)
43. Yodzis P. 1988 The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* **69**, 508–515. (doi: 10.2307/1940449)
44. Legagneux P *et al.* 2014 Arctic ecosystem structure and functioning shaped by climate and herbivore body size. *Nat. Clim. Change* **4**, 379–383. (doi:10.1038/nclimate2168)
45. Kassen R. 2002 The experimental evolution of specialists, generalists, and the maintenance of diversity. *J. Evol. Biol.* **15**, 173–190. (doi:10.1046/j.1420-9101.2002.00377.x)
46. Fortuna MA, Albaladejo RG, Fernández L, Aparicio A, Bascompte J. 2009 Networks of spatial genetic variation across species. *Proc. Natl. Acad. Sci. USA* **106**, 19 044–19 049. (doi:10.1073/pnas.09077 04106)
47. Carstensen DW, Dalsgaard B, Svenning JC, Rahbek C, Fjeldså J, Sutherland WJ, Olesen JM. 2012 Biogeographical modules and island roles: a comparison of Wallacea and the West Indies. *J. Biogeogr.* **39**, 739–749. (doi:10.1111/j.1365-2699.2011.02628.x)
48. Bellisario B, Cerfolli F, Nascetti G. 2010 Spatial network structure and robustness of detritus-based communities in a patchy environment. *Ecol. Res.* **25**, 813–821. (doi:10.1007/s11284-010-0711-5)
49. Olesen JM, Bascompte J, Dupont YL, Jordano P. 2007 The modularity of pollination networks. *Proc. Natl. Acad. Sci. USA* **104**, 19 891–19 896. (doi:10.1073/pnas.0706375104)
50. Dupont YL, Olesen JM. 2009 Ecological modules and roles of species in heathland plant–insect flower visitor networks. *J. Anim. Ecol.* **78**, 346–353. (doi:10.1111/j.1365-2656.2008.01501.x)
51. Frank KT, Petrie B, Choi JS, Leggett WC. 2005 Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**, 1621–1623. (doi:10.1126/science.1113075)
52. Fauchald P, Barret RT, Bustens JO, Erikstad KE, Nøttestad L, Skern-Mauritzen M, Vikebø FB. 2015 Sjøfugl og marine økosystemer. Status for sjøfugl og sjøfuglenes næringsgrunnlag i Norge og på Svalbard. Norsk institutt for naturforskning (NINA) Rapport, p. 38. Tromsø.
53. Bogstad B, Gjøsæter H, Haug T, Lindstrøm U. 2015 A review of the battle for food in the Barents Sea: cod vs. marine mammals. *Front. Ecol. Evol.* **3**. (doi:10.3389/fevo.2015.00029)

Electronic supporting material

Climate change alters the structure of Arctic marine food webs due to poleward shifts of boreal generalists

Susanne Kortsch, Raul Primicerio, Maria Fossheim, Andrey V. Dolgov, and Michaela Aschan

Appendix S1. Detailed description of the study regions and subsampling of the marine food webs

(a) *Barents Sea*

The Barents Sea is an open arcto-boreal shelf sea and is the largest marginal shelf sea in the Arctic Ocean (figure S1). The Barents Sea ecosystem is profoundly influenced by the inflow of relatively warm and saline atlantic water ($T > 3^{\circ}\text{C}$, $S > 35 \text{‰}$) in the south-west, and arctic water masses ($T < 0^{\circ}\text{C}$, $34.3 \text{‰} \leq S \leq 34.8 \text{‰}$) in the North. The mixing of atlantic and arctic water masses at the polar front, as well as the presence of the marginal ice zone, strongly influence biological production. The Barents Sea is one of the most productive marine ecosystems in the world [1]. In the Arctic, the Barents Sea accounts for 49 % of total pan-arctic shelf primary production and supports some of the largest fish stocks of the world including north-east arctic cod (*Gadus morhua*), polar cod (*Boreogadus saida*), capelin (*Mallotus villosus*) and herring (*Clupea harengus*) [2, 3]. Due to easy access, high productivity and its importance for fisheries, the Barents Sea is one of the best studied marine ecosystems in the Arctic [4]. Since 2004, Norwegian and Russian research institutions have sampled taxa from the entire food web in a joint effort to map the whole ecosystem [5].

(b) Boreal and arctic study regions of the Barents Sea

We have defined the boreal (186 400 km²) and arctic (304 067 km²) study regions based on hydrology and species distributions (figure S2a). To capture a good snapshot representation of a boreal and an arctic food webs of the Barents Sea, we chose areas south-west and north-east of the polar front, which is the main hydrological demarcation separating boreal and arctic regions of the Barents Sea (figure S2b). The exact position of the polar front varies from year to year and is most variable in the east depending on the strength of the atlantic water inflow [6]. The past decade (2000-2010) has been the warmest on record and warmer and more salty atlantic water masses have extended further north and north-east into the Barents Sea resulting in a contraction of the area covered by arctic water masses [7, 8]. In addition to hydrological data, we used fish abundance data to define the position of the two regions [9].

(c) Occurrence of fish and epibenthos

In this study, presence and absence of fish was integrated over the early sampling period 2004-2007 to specify occurrence of species within study areas. The early years of the sampling were chosen in order to capture a snapshot of the arctic food web prior to the pronounced distributional shifts of large fish driven by rapid warming [2, 10]. After 2007, the surveys reveal how boreal fish are moving even further north-east into the arctic regions of the Barents Sea [2,11]. Data on the occurrence of epibenthos are from 2011. To overcome the problem of including rare and only occasionally sampled fish and epibenthos, we used distribution maps and additional abundance information for sub-sampling among these groups (figure S2b). In the boreal study region, fish were sampled at 308 stations (2004-2007) and epibenthos at 38 stations (2011). In the arctic study region, fish were sampled at 327 stations and epibenthos at 50 (figure S1b). Three selection criteria were formulated for each

trophospecies: 1) mean abundance of a taxon within study areas; 2) max abundance of a taxon within study areas; and 3) proportion of stations in which a taxon was found. A trophospecies was included in the food web of a given area if it was selected based on at least one of the three selection criteria. In some cases, the quantitative selection criteria had to be complemented with knowledge of species spatial distribution prior to 2004. For example, we chose not to include cod and haddock in the arctic food web because these two taxa were hardly present in the arctic study region prior to warming. Likewise, we excluded polar cod from the boreal food webs, although a few individuals can sometimes be caught in the boreal region of the Barents Sea.

(d) *Food web data: shortcomings and strengths*

Trophospecies included in the food web database (meta-web) were selected according to at least one of the following criteria: 1) abundance, 2) spatial distribution and 3) existing knowledge of trophic relationships. Rare species were not included. In our food webs, individual trophospecies usually correspond to taxonomic species, but can sometimes refer to higher taxonomic groups, e.g. genus, family, and class. Other large aggregations include the basal taxa such as phytoplankton, diatoms, heterotroph flagellates or bryozoans. While compiling the database, we made considerable efforts to obtain a balanced representation of the different functional groups and their feeding links. Yet, we are aware that, for some of the arctic taxa, research and literature is sparser and this may have led to an underestimation of their feeding links.

To date, most marine food webs are systematically biased towards higher trophic levels because of incomplete diet information and poor sampling of basal species. We acknowledge that a better resolution at the basal level would increase the percentage of low trophic level

species and decrease the relative proportion of intermediate species. Expansion of the basal compartment (particularly phytoplankton and benthos) should be prioritized to reduce this bias and to improve the representation of the complexity in future marine food webs.

Although historically food webs have under-represented the number of species and their links [12], recent compilations of food webs are becoming increasingly comprehensive, with higher resolution, level of detail and scale [13]. Our Barents Sea food webs are examples of highly resolved ecological networks, and unlike most comparative food web studies, the level of trophospecies aggregation between the study regions is identical. This implies that dissimilarities observed between Boreal and Arctic food webs here cannot be attributed to differences in the classification and aggregation of trophospecies, but must be attributed to differences in species composition and link configuration of the regional food webs.

The dataset file of the meta-web for the whole Barents Sea can be downloaded from the *Ecological archives* website [5], while the boreal and the arctic Barents Sea food web files of the present study can be downloaded from the Dryad repository (doi:10.5061/dryad.73r6j).

References

1. Carmack, E., Wassmann, P., 2006 Food webs and physical-biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. *Progr. Oceanogr.* **71**, 446-477. (doi:10.1016/j.pocean.2006.10.004)
2. Michalsen, K., Dalpadado, P., Eriksen, E., Gjørseter, H., Ingvaldsen, R. B., Johannesen, E., Jørgensen, L. L., Knutsen, T., Prozorkevich, D., Skern-Mauritzen, M. 2013 Marine living resources of the Barents Sea–Ecosystem understanding and monitoring in a climate change perspective. *Mar. Biol. Res.* **9**, 932-947. (doi:10.1080/17451000.2013.775459)
3. Sakshaug, E., Johnsen, G. H., Kovacs, K. M. 2009 *Ecosystem Barents Sea*, Tapir Academic Press. pp. 57-81.

4. Wassmann, P., Duarte, C. M., Agusti, S., Sejr, M. K. 2011 Footprints of climate change in the Arctic marine ecosystem. *Glob. Change Biol.* **17** (2), 1235-1249. (doi:10.1111/j.1365-2486.2010.02311.x)
5. Planque, B., Primicerio, R., Michalsen, K., Aschan, M., Certain, G., Dalpadado, P., Gjøsæter, H., Hansen, C., Johannesen, E., Jørgensen, L.L., Kolsum, I., Kortsch, S., Leclerc, L-M., Omli, L., Skern-Mauritzen, M., Wiedmann, M. 2014 Who eats whom in the Barents Sea: a food web topology from plankton to whales: Ecological Archives E095-124. *Ecology* **95**, 1430-1430. (doi:10.1890/13-1062.1)
6. Loeng, H., 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. (doi:10.1016/j.dsr2.2007.08.013)
7. Smedsrud, L.H., Ingvaldsen, R., Nilsen, J., Skagseth, Ø. 2010 Heat in the Barents Sea: transport, storage, and surface fluxes. *Ocean Sci.* **6**, 219-234. (doi:10.5194/os-6-219-2010)
8. Ellingsen, I. H., Dalpadado, P., Slagstad, D., Loeng, H. 2008 Impact of climatic change on the biological production in the Barents Sea. *Clim. change* **87**, 155-175. (doi: 10.1007/s10584-007-9369-6)
9. Fossheim M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., Dolgov, A. V. 2015 Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Clim. Change* (doi:10.1038/nclimate2647)
10. Wiedmann, M. A., Aschan, M., Certain, G., Dolgov, A., Greenacre, M., Johannesen, E., Planque, B., Primicerio, R. 2014 Functional diversity of the Barents Sea fish community. *Mar. Ecol. Prog. Ser.* **495**, 205-218. (doi:103354/meps10558)
11. Hollowed, A.B., Sundby, S. 2014 Change is coming to the northern oceans. *Science* **344**, 1084-1085. (doi: DOI: 10.1126/science.1251166)
12. Polis, G. A. 1991 Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am. Nat.* 123-155.
13. Dunne, J. A., Lafferty, K. D., Dobson A. P., Hechinger, R. F., Kuris, A. M., Martinez, N. D., McLaughlin, J. P., Mouritsen, K. N., Poulin, R., Reise, K. 2013 Parasites affect food web structure primarily through increased diversity and complexity. *PLoS Biol.* **11**, e1001579. (doi: 10.1371/journal.pbio.1001579)

Appendix S2. Supplementary figures and tables

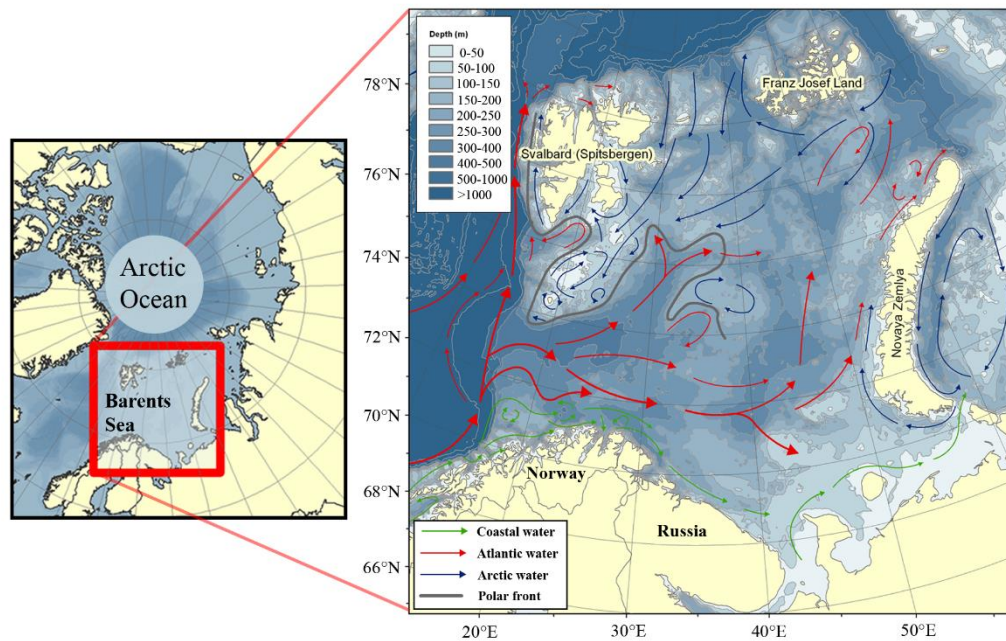


Figure S1. Map of the Barents Sea (to the right) and of its location (to the left) in the Arctic. The topography is indicated with the blue gradients, see legend in the top-left corner. The atlantic (red) and arctic (blue) ocean currents within the Barents Sea are indicated with arrows, see legend in the bottom-left corner.

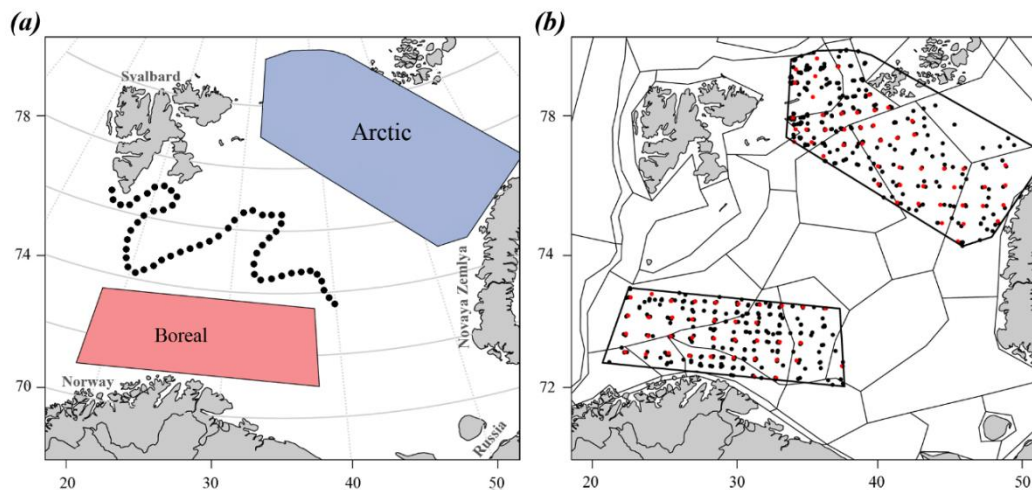


Figure S2. (a) Location of the boreal (red) and arctic (blue) study regions within the Barents Sea. The black dotted line indicates the approximate position of the polar front, separating atlantic and arctic water masses. (b) Location of the sampling stations for fish (black dots) and epibenthos (red dots) within the boreal and the arctic study regions used to subsample the boreal and the arctic food webs. The remaining trophospecies (basal taxa, zooplankton, benthic infauna, sea birds and marine mammals) were assigned to the study regions via their presence/absence within the indicated polygons.

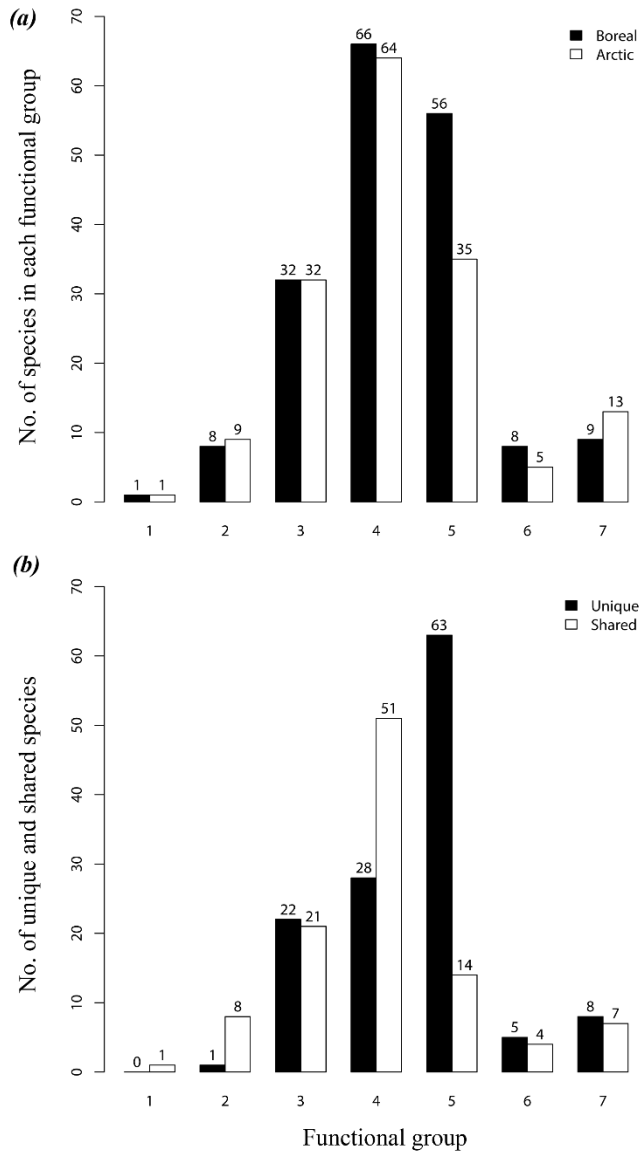


Figure S3. (a) Number of trophospecies in each functional group of the boreal (black bars) and arctic (white bars) food webs. (b) Number of unique (black bars) and shared (white bars) trophospecies between the boreal and arctic food web. The functional groups are: 1=detritus; 2=basal taxa; 3=zooplankton; 4=benthos; 5=fish; 6=sea birds; 7=marine mammals.

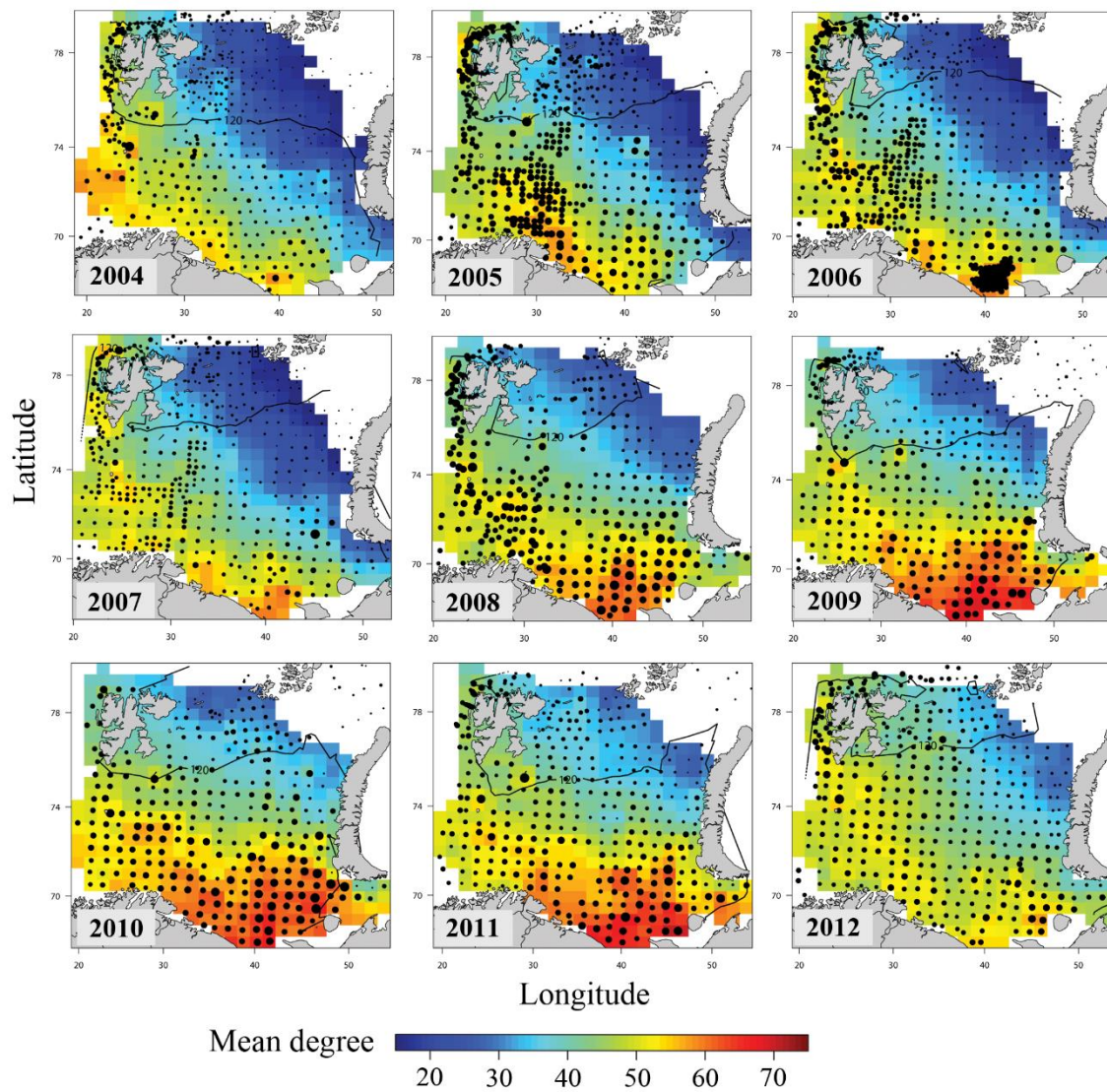


Figure S4. Barents Sea maps of the yearly mean degree centrality (number of feeding links) of fish during the time period 2004 to 2012. The dots indicate the position of sampling stations (~400) and the size of the dots is proportional to the mean fish degree at the station. The coloured surface (colour code shown in the legend) indicates the mean degree of fish spatially interpolated on a regular grid. North of the 120 day isolines (black lines) sea ice was present for more than 120 days during the year.

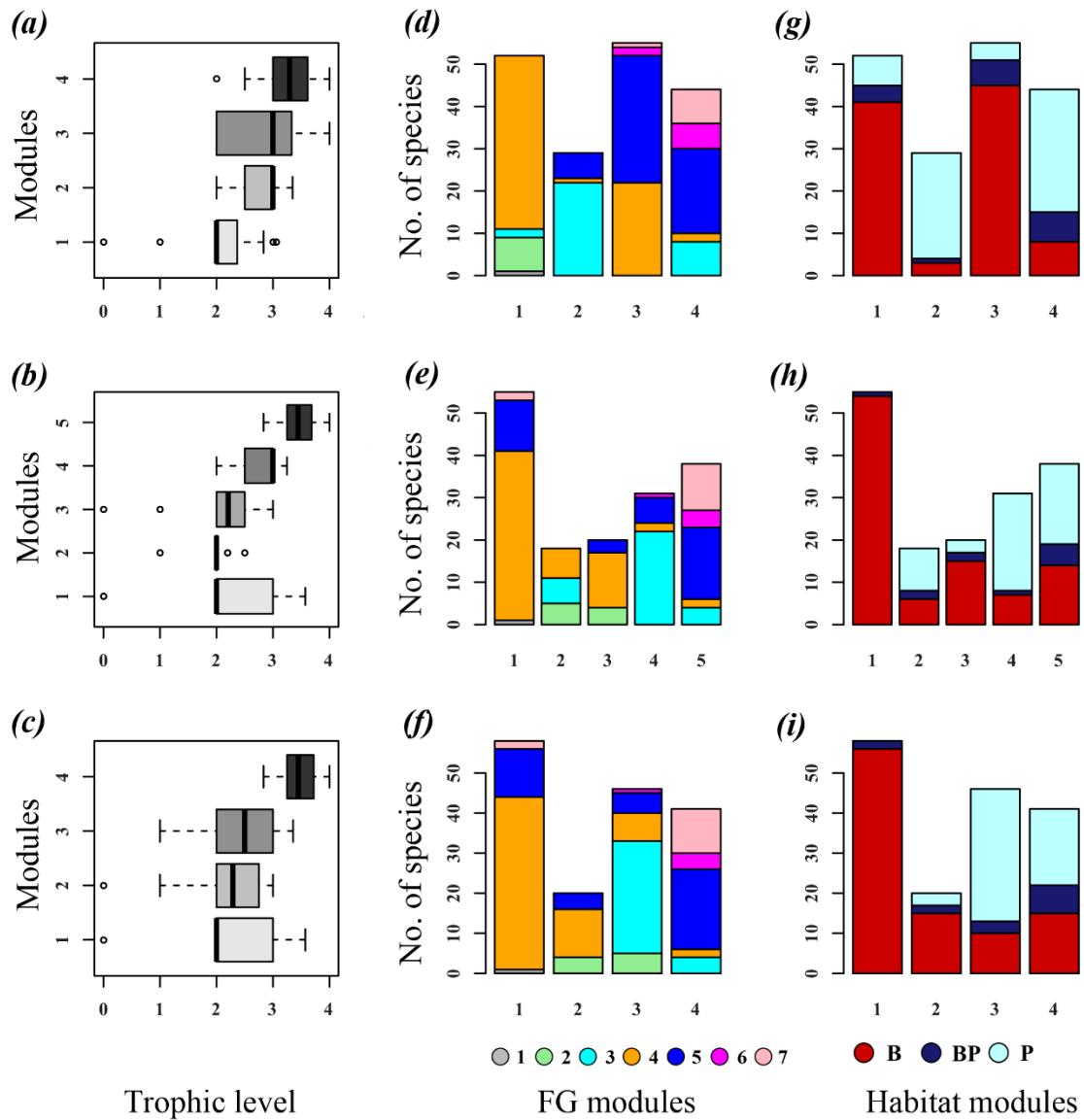


Figure S5. Boxplot of the trophic level of trophospecies within each module in (a) the boreal, (b) the arctic and (c) the arctic II food webs. Bar plot of the number of species within each module of (d) the boreal, (e) the arctic, (f) and the arctic II food webs. The colours in the bar plots indicate the functional group (FG) affiliation: grey=detritus (1); green=basal taxa (2); cyan=zooplankton (3); orange=benthos (4); blue=fish (5); magenta=sea birds (6); light pink=marine mammals (7). Bar plots of (g) the boreal, (h) the arctic, and (i) the arctic II food web showing the frequency of benthic=red, benthic-pelagic=dark-blue and pelagic=light-blue trophospecies within each module.

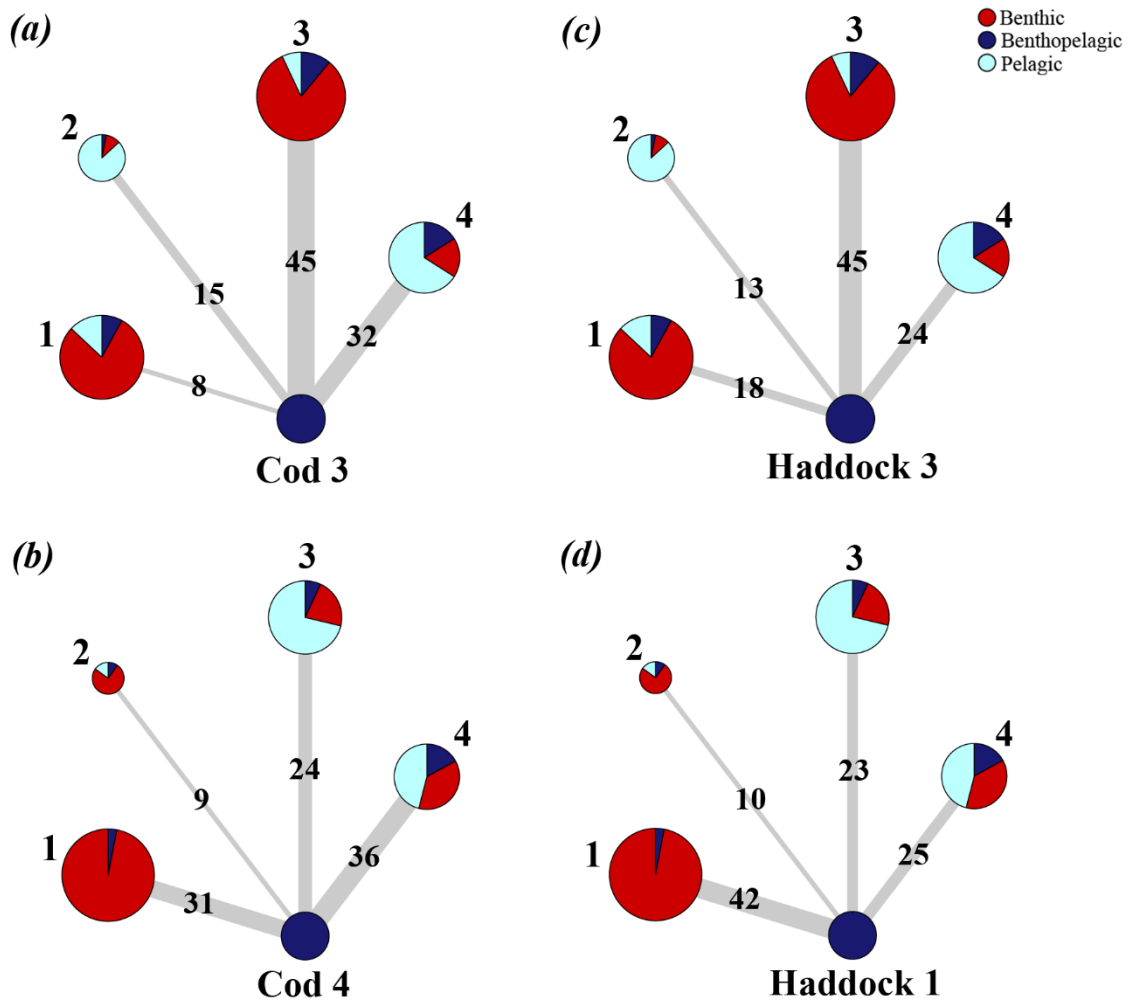


Figure S6. The module affiliation of the two network hubs, cod and haddock, and their distribution of links to species within their own module and to species in other modules for the boreal and the arctic II food web. Linkage structure of (a) cod in the boreal food web, (b) cod in the arctic II food web, (c) haddock in the boreal food web, and (d) haddock in the arctic II food web. The number next to the fish name indicates which module cod and haddock belong to. The number on the edges (grey lines) indicate how many links cod and haddock have to species in these modules. Bi-directional links (mutual predation links) are only counted once. The colored pie-charts show the proportion of pelagic (light blue), benthic (red) and benthopelagic (blue) species within each module.

Table S1. List of taxa (in alphabetical order within each functional group) included in the boreal region of the Barents Sea, and their functional affiliation, habitat use, degree (number of trophic interactions) and topological role.

Index	Taxon	Functional group	Habitat	Degree	Topological role
1	Detritus	1 Detritus	Benthopelagic	53	Module hub
2	Autothroph_flagellat	2 Basal taxa	Pelagic	22	Peripheral
3	Bacteria_indet	2 Basal taxa	Benthopelagic	13	Peripheral
4	Diatom	2 Basal taxa	Benthopelagic	33	Peripheral
5	Heterotroph_flagellat	2 Basal taxa	Pelagic	21	Peripheral
6	Macroalgae	2 Basal taxa	Benthic	4	Peripheral
7	Mixotroph_flagellates	2 Basal taxa	Pelagic	5	Peripheral
8	Phytoplankton_indet	2 Basal taxa	Pelagic	47	Module connector
9	Protozooplankton	2 Basal taxa	Pelagic	13	Peripheral
10	<i>Acartia_spp</i>	3 Zooplankton	Pelagic	18	Module connector
11	<i>Aglantha_digitale</i>	3 Zooplankton	Pelagic	6	Peripheral
12	<i>Aurelia_aurita</i>	3 Zooplankton	Pelagic	12	Peripheral
13	<i>Beroë_sp</i>	3 Zooplankton	Pelagic	14	Peripheral
14	<i>Bolinopsis_infundibulum</i>	3 Zooplankton	Pelagic	14	Peripheral
15	<i>Calanus_finmarchicus</i>	3 Zooplankton	Pelagic	52	Module connector
16	<i>Calanus_glacialis</i>	3 Zooplankton	Pelagic	39	Module connector
17	<i>Calanus_hyperboreus</i>	3 Zooplankton	Pelagic	43	Module connector
18	<i>Clione_limacina</i>	3 Zooplankton	Pelagic	9	Peripheral
19	<i>Cyanea_capillata</i>	3 Zooplankton	Pelagic	21	Peripheral
20	<i>Dimophyes_arctica</i>	3 Zooplankton	Pelagic	2	Peripheral
21	<i>Eukrohnia_hamata</i>	3 Zooplankton	Pelagic	10	Peripheral
22	<i>Fritillaria_borealis</i>	3 Zooplankton	Pelagic	4	Peripheral
23	<i>Limacina_helicina</i>	3 Zooplankton	Pelagic	12	Peripheral
24	<i>Limacina_retroversa</i>	3 Zooplankton	Pelagic	12	Peripheral
25	<i>Meganyctiphanes_norvegica</i>	3 Zooplankton	Pelagic	42	Module connector
26	<i>Metridia_longa</i>	3 Zooplankton	Pelagic	26	Module connector
27	<i>Nematoscelis_megalops</i>	3 Zooplankton	Pelagic	3	Peripheral
28	<i>Oikopleura_dioica</i>	3 Zooplankton	Pelagic	5	Peripheral
29	<i>Oikopleura_spp</i>	3 Zooplankton	Pelagic	12	Module connector
30	<i>Oithona_similis</i>	3 Zooplankton	Pelagic	6	Peripheral
31	<i>Oithona_spinirostris/atlantica</i>	3 Zooplankton	Pelagic	26	Module connector
32	<i>Oncaea_borealis</i>	3 Zooplankton	Pelagic	9	Peripheral
33	<i>Pareuchaeta_norvegica</i>	3 Zooplankton	Pelagic	11	Peripheral
34	<i>Pareuchaeta_spp</i>	3 Zooplankton	Pelagic	9	Peripheral
35	<i>Pseudocalanus_spp</i>	3 Zooplankton	Pelagic	24	Peripheral
36	<i>Sagitta_spp</i>	3 Zooplankton	Pelagic	33	Module connector
37	<i>Sarsia_spp</i>	3 Zooplankton	Pelagic	6	Peripheral
38	<i>Themisto_abyssorum</i>	3 Zooplankton	Pelagic	32	Module connector
39	<i>Thysanoessa_inermis</i>	3 Zooplankton	Pelagic	45	Module connector
40	<i>Thysanoessa_longicaudata</i>	3 Zooplankton	Pelagic	33	Peripheral
41	<i>Thysanoessa_raschii</i>	3 Zooplankton	Pelagic	38	Peripheral
42	<i>Actiniaria_g_sp</i>	4 Benthos	Benthic	11	Module connector

43	<i>Aglaophamus_malmgreni</i>	4 Benthos	Benthic	6	Peripheral
44	<i>Aphelochaeta_marioni</i>	4 Benthos	Benthic	6	Peripheral
45	<i>Arrhis_phyllonyx</i>	4 Benthos	Benthic	8	Module connector
46	Ascidacea_g_sp	4 Benthos	Benthic	6	Peripheral
47	Asellota_indet	4 Benthos	Benthic	7	Peripheral
48	<i>Astarte_sp</i>	4 Benthos	Benthic	10	Peripheral
49	<i>Asterias_rubens</i>	4 Benthos	Benthic	13	Peripheral
50	<i>Balanus_sp</i>	4 Benthos	Benthic	11	Peripheral
51	<i>Bathyarca_galacialis</i>	4 Benthos	Benthic	3	Module connector
52	Bryozoa_indet	4 Benthos	Benthic	4	Peripheral
53	Benthos_larvae	4 Benthos	Benthopelagic	8	Module connector
54	<i>Buccinum_sp</i>	4 Benthos	Benthic	9	Peripheral
55	<i>Chaetozone_sp</i>	4 Benthos	Benthic	5	Peripheral
56	<i>Chlamys_islandica</i>	4 Benthos	Benthic	7	Peripheral
57	<i>Chone_sp</i>	4 Benthos	Benthic	4	Peripheral
58	<i>Ciona_intestinalis</i>	4 Benthos	Benthic	6	Peripheral
59	Cirratulidae_indet	4 Benthos	Benthic	6	Peripheral
60	<i>Colus_sp</i>	4 Benthos	Benthic	4	Peripheral
61	<i>Ctenodiscus_crispatus</i>	4 Benthos	Benthic	8	Peripheral
62	<i>Cucumaria_froncosa</i>	4 Benthos	Benthic	9	Peripheral
63	<i>Erythrospis_sp</i>	4 Benthos	Benthic	12	Peripheral
64	Euclymeninae_indet	4 Benthos	Benthic	3	Peripheral
65	Foraminifera	4 Benthos	Benthic	16	Peripheral
66	<i>Galathowenia_sp</i>	4 Benthos	Benthic	3	Peripheral
67	Gammaridae_indet	4 Benthos	Benthic	32	Peripheral
68	<i>Geodia_sp</i>	4 Benthos	Benthic	3	Peripheral
69	<i>Gonatus_fabricii</i>	4 Benthos	Pelagic	33	Peripheral
70	<i>Heteromastus_filiformis</i>	4 Benthos	Benthic	4	Peripheral
71	<i>Hyas_sp</i>	4 Benthos	Benthic	12	Peripheral
72	Hydrozoa_indet	4 Benthos	Benthic	1	Peripheral
73	<i>Lumbriclymene_minor</i>	4 Benthos	Benthic	7	Peripheral
74	<i>Lumbrineris_sp</i>	4 Benthos	Benthic	18	Peripheral
75	<i>Macoma_sp</i>	4 Benthos	Benthic	9	Peripheral
76	<i>Maldane_sarsi</i>	4 Benthos	Benthic	5	Peripheral
77	<i>Mendicula_ferruginosa</i>	4 Benthos	Benthic	4	Module connector
78	<i>Molpadia_borealis</i>	4 Benthos	Benthic	11	Peripheral
79	<i>Myriochele_herri</i>	4 Benthos	Benthic	1	Peripheral
80	<i>Nephtheidae_sp</i>	4 Benthos	Benthic	3	Peripheral
81	<i>Nyctiphanes_couchii</i>	4 Benthos	Benthic	7	Module connector
82	<i>Ophiopholis_aculeata</i>	4 Benthos	Benthic	19	Peripheral
83	<i>Ophiura_sp</i>	4 Benthos	Benthic	30	Peripheral
84	Ostracoda_indet	4 Benthos	Benthic	22	Module connector
85	<i>Pagurus_sp</i>	4 Benthos	Benthic	15	Peripheral
86	<i>Pandalus_borealis</i>	4 Benthos	Benthic	59	Module connector
87	<i>Paralithodes_camtschaticus</i>	4 Benthos	Benthic	55	Module hub
88	<i>Paramphinoe_jeffreysii</i>	4 Benthos	Benthic	3	Peripheral

89	<i>Phascolion_strombus</i>	4 Benthos	Benthic	3	Peripheral
90	Polychaeta	4 Benthos	Benthic	36	Peripheral
91	Polynoidae_indet	4 Benthos	Benthic	17	Peripheral
92	<i>Pontaster_tenuispinus</i>	4 Benthos	Benthic	3	Peripheral
93	<i>Pontophilus_norvegicus</i>	4 Benthos	Benthic	10	Peripheral
94	Porifera_g_sp	4 Benthos	Benthic	8	Peripheral
95	<i>Prionospio_cirrifera</i>	4 Benthos	Benthic	4	Peripheral
96	<i>Rhachotropis_macropus</i>	4 Benthos	Benthic	9	Module connector
97	<i>Rossia_sp</i>	4 Benthos	Benthic	15	Peripheral
98	<i>Sabinea_sp</i>	4 Benthos	Benthic	17	Peripheral
99	<i>Scalibregma_inflatum</i>	4 Benthos	Benthic	6	Peripheral
100	<i>Similipecten_greenlandicus</i>	4 Benthos	Benthic	5	Peripheral
101	<i>Spiophanes_kroeyeri</i>	4 Benthos	Benthic	4	Peripheral
102	Spirorbidae_indet	4 Benthos	Benthic	2	Peripheral
103	<i>Stichopus_tremulus</i>	4 Benthos	Benthic	8	Peripheral
104	<i>Strongylocentrotus_sp</i>	4 Benthos	Benthic	13	Peripheral
105	<i>Terebellides_stroemi</i>	4 Benthos	Benthic	10	Peripheral
106	<i>Thyasira_gouldi</i>	4 Benthos	Benthic	6	Peripheral
107	<i>Yoldiella_solidula</i>	4 Benthos	Benthic	8	Peripheral
108	<i>Agonus_cataphractus</i>	5 Fish	Benthic	11	Peripheral
109	<i>Amblyraja_radiata</i>	5 Fish	Benthic	49	Peripheral
110	<i>Ammodytes_spp</i>	5 Fish	Benthopelagic	38	Module connector
111	<i>Anarhichas_denticulatus</i>	5 Fish	Benthic	22	Peripheral
112	<i>Anarhichas_lupus</i>	5 Fish	Benthic	33	Module connector
113	<i>Anarhichas_minor</i>	5 Fish	Benthic	27	Peripheral
114	<i>Anisarchus_medius</i>	5 Fish	Benthic	4	Peripheral
115	<i>Arctozenus_risso</i>	5 Fish	Pelagic	7	Peripheral
116	<i>Argentina_sp</i>	5 Fish	Pelagic	11	Peripheral
117	<i>Artediellus_atlanticus</i>	5 Fish	Benthic	10	Peripheral
118	<i>Bathyraja_spinicauda</i>	5 Fish	Benthic	16	Peripheral
119	<i>Benthoosema_glaciale</i>	5 Fish	Pelagic	6	Peripheral
120	<i>Brosme_brosme</i>	5 Fish	Benthic	13	Peripheral
121	<i>Careproctus_sp</i>	5 Fish	Benthopelagic	8	Peripheral
122	<i>Clupea_harengus</i>	5 Fish	Pelagic	58	Module connector
123	<i>Cottunculus_microps</i>	5 Fish	Benthic	6	Peripheral
124	<i>Cyclopterus_lumpus</i>	5 Fish	Benthopelagic	5	Peripheral
125	<i>Enchelyopus_cimbrius</i>	5 Fish	Benthic	4	Peripheral
126	<i>Etimopterus_spinax</i>	5 Fish	Benthic	5	Peripheral
127	<i>Gadiculus_argenteus</i>	5 Fish	Pelagic	14	Peripheral
128	<i>Gadus_morhua</i>	5 Fish	Benthopelagic	112	Network hub
129	<i>Gaidropsarus_argentatus</i>	5 Fish	Benthic	9	Peripheral
130	<i>Gasterosteus_aculeatus</i>	5 Fish	Pelagic	6	Peripheral
131	<i>Glyptocephalus_cynoglossus</i>	5 Fish	Benthic	8	Peripheral
132	<i>Hippoglossus_hippoglossus</i>	5 Fish	Benthic	22	Peripheral
133	<i>Hippoglossoides_platessoides</i>	5 Fish	Benthic	28	Peripheral
134	<i>Leptoclinus_maculatus</i>	5 Fish	Benthic	4	Peripheral

135	<i>Limanda limanda</i>	5 Fish	Benthic	18	Peripheral
136	<i>Liparis montagui</i>	5 Fish	Benthic	10	Module connector
137	<i>Lumpenus lampretaeformis</i>	5 Fish	Benthic	17	Module connector
138	<i>Lycodes esmarkii</i>	5 Fish	Benthic	9	Peripheral
139	<i>Lycodes gracilis</i>	5 Fish	Benthic	4	Peripheral
140	<i>Lycodes pallidus</i>	5 Fish	Benthic	15	Peripheral
141	<i>Macrourus berglax</i>	5 Fish	Benthic	20	Peripheral
142	<i>Mallotus villosus</i>	5 Fish	Pelagic	46	Peripheral
143	<i>Maurolicus muelleri</i>	5 Fish	Pelagic	12	Peripheral
144	<i>Melanogrammus aeglefinus</i>	5 Fish	Benthopelagic	88	Network hub
145	<i>Merlangius merlangus</i>	5 Fish	Benthopelagic	34	Module connector
146	<i>Micromesistius poutassou</i>	5 Fish	Pelagic	55	Module connector
147	<i>Microstomus kitt</i>	5 Fish	Benthic	4	Module connector
148	<i>Molva molva</i>	5 Fish	Benthic	11	Peripheral
149	Fish_larvae	5 Fish	Benthopelagic	30	Module connector
150	<i>Pleuronectes platessa</i>	5 Fish	Benthic	34	Peripheral
151	<i>Pollachius pollachius</i>	5 Fish	Pelagic	18	Peripheral
152	<i>Pollachius virens</i>	5 Fish	Pelagic	47	Peripheral
153	<i>Rajella fyllae</i>	5 Fish	Benthic	8	Peripheral
154	<i>Reinhardtius hippoglossoides</i>	5 Fish	Benthopelagic	36	Peripheral
155	<i>Scomber scombrus</i>	5 Fish	Pelagic	25	Peripheral
156	<i>Sebastes norvegicus</i>	5 Fish	Benthopelagic	23	Peripheral
157	<i>Sebastes mentella</i>	5 Fish	Benthopelagic	62	Module connector
158	<i>Sebastes spp</i>	5 Fish	Benthopelagic	29	Peripheral
159	<i>Sebastes viviparus</i>	5 Fish	Benthic	8	Module connector
160	<i>Somniosus microcephalus</i>	5 Fish	Benthopelagic	39	Peripheral
161	<i>Squalus acanthias</i>	5 Fish	Benthopelagic	14	Peripheral
162	<i>Triglops murrayi</i>	5 Fish	Benthic	10	Peripheral
163	<i>Trisopterus esmarkii</i>	5 Fish	Pelagic	35	Module connector
164	<i>Fratercula arctica</i>	6 Birds	Pelagic	10	Peripheral
165	<i>Fulmarus glacialis</i>	6 Birds	Pelagic	27	Peripheral
166	<i>Larus argentatus</i>	6 Birds	Pelagic	5	Peripheral
167	<i>Larus hyperboreus</i>	6 Birds	Pelagic	6	Peripheral
168	<i>Larus marinus</i>	6 Birds	Pelagic	5	Peripheral
169	<i>Rissa tridactyla</i>	6 Birds	Pelagic	10	Peripheral
170	<i>Uria aalge</i>	6 Birds	Pelagic	7	Peripheral
171	<i>Uria lomvia</i>	6 Birds	Pelagic	3	Peripheral
172	<i>Balaenoptera acutorostrata</i>	7 Mammals	Pelagic	21	Peripheral
173	<i>Balaenoptera physalus</i>	7 Mammals	Pelagic	22	Peripheral
174	<i>Erignathus barbatus</i>	7 Mammals	Benthic	24	Peripheral
175	<i>Lagenorhynchus albirostris</i>	7 Mammals	Pelagic	8	Peripheral
176	<i>Megaptera novaeangliae</i>	7 Mammals	Pelagic	22	Peripheral
177	<i>Orcinus orca</i>	7 Mammals	Pelagic	9	Peripheral
178	<i>Pagophilus groenlandicus</i>	7 Mammals	Benthopelagic	17	Peripheral
179	<i>Phocoena phocoena</i>	7 Mammals	Pelagic	32	Peripheral
180	<i>Physeter macrocephalus</i>	7 Mammals	Pelagic	2	Peripheral

Table S2. List of taxa (in alphabetical order within each functional group) included in the Arctic region of the Barents Sea, and their functional affiliation, habitat use, degree (number of trophic interactions) and topological role.

Index	Taxon	Functional group	Habitat	Degree	Topological role
1	Detritus	1 Detritus	Benthopelagic	54	Module hub
2	Autotroph_flagellat	2 Basal taxa	Pelagic	15	Module connector
3	Bacteria_indet	2 Basal taxa	Benthopelagic	14	Peripheral
4	Diatom	2 Basal taxa	Benthopelagic	23	Peripheral
5	Heterotroph_flagellat	2 Basal taxa	Pelagic	13	Module connector
6	Ice_algae	2 Basal taxa	Pelagic	4	Peripheral
7	Macroalgae	2 Basal taxa	Benthic	3	Peripheral
8	Mixotroph_flagellates	2 Basal taxa	Pelagic	3	Peripheral
9	Phytoplankton_indet	2 Basal taxa	Pelagic	44	Network hub
10	Protozooplankton	2 Basal taxa	Pelagic	13	Peripheral
11	<i>Aglantha_digitale</i>	3 Zooplankton	Pelagic	2	Peripheral
12	<i>Apherusa_glacialis</i>	3 Zooplankton	Pelagic	8	Module connector
13	<i>Bolinopsis_infundibulum</i>	3 Zooplankton	Pelagic	7	Peripheral
14	<i>Calanus_finmarchicus</i>	3 Zooplankton	Pelagic	37	Module connector
15	<i>Calanus_glacialis</i>	3 Zooplankton	Pelagic	32	Module connector
16	<i>Calanus_hyperboreus</i>	3 Zooplankton	Pelagic	37	Module connector
17	<i>Clione_limacina</i>	3 Zooplankton	Pelagic	6	Peripheral
18	<i>Cyanea_capillata</i>	3 Zooplankton	Pelagic	16	Peripheral
19	<i>Dimophyes_arctica</i>	3 Zooplankton	Pelagic	2	Peripheral
20	<i>Eukrohnia_hamata</i>	3 Zooplankton	Pelagic	8	Peripheral
21	<i>Euphysa_flammea</i>	3 Zooplankton	Pelagic	6	Peripheral
22	<i>Fritillaria_borealis</i>	3 Zooplankton	Pelagic	4	Peripheral
23	<i>Gammarus_wilkitzkii</i>	3 Zooplankton	Pelagic	21	Module connector
24	<i>Limacina_helicina</i>	3 Zooplankton	Pelagic	15	Peripheral
25	<i>Mertensia_ovum</i>	3 Zooplankton	Pelagic	6	Peripheral
26	<i>Metridia_longa</i>	3 Zooplankton	Pelagic	21	Peripheral
27	<i>Metridia_lucens</i>	3 Zooplankton	Pelagic	4	Peripheral
28	<i>Microcalanus_spp</i>	3 Zooplankton	Pelagic	12	Peripheral
29	<i>Oikopleura_spp</i>	3 Zooplankton	Pelagic	7	Module connector
30	<i>Oikopleura_vanhoeffeni</i>	3 Zooplankton	Pelagic	5	Module connector
31	<i>Oithona_similis</i>	3 Zooplankton	Pelagic	7	Peripheral
32	<i>Onisimus_glacialis</i>	3 Zooplankton	Pelagic	9	Module connector
33	<i>Onisimus_nanseni</i>	3 Zooplankton	Pelagic	8	Module connector
34	<i>Pareuchaeta_glacialis</i>	3 Zooplankton	Pelagic	6	Peripheral
35	<i>Pareuchaeta_spp</i>	3 Zooplankton	Pelagic	10	Peripheral
36	<i>Pseudocalanus_spp</i>	3 Zooplankton	Pelagic	21	Peripheral
37	<i>Sagitta_spp</i>	3 Zooplankton	Pelagic	21	Peripheral
38	<i>Sarsia_spp</i>	3 Zooplankton	Pelagic	4	Peripheral
39	<i>Themisto_abyssorum</i>	3 Zooplankton	Pelagic	29	Peripheral
40	<i>Themisto_libellula</i>	3 Zooplankton	Pelagic	36	Peripheral
41	<i>Thysanoessa_inermis</i>	3 Zooplankton	Pelagic	33	Peripheral
42	<i>Thysanoessa_longicaudata</i>	3 Zooplankton	Pelagic	24	Peripheral

43	<i>Actiniaria_g_sp</i>	4 Benthos	Benthic	7	Peripheral
44	<i>Aglaphamus_malmgreni</i>	4 Benthos	Benthic	3	Peripheral
45	<i>Aphelochaeta_marioni</i>	4 Benthos	Benthic	4	Peripheral
46	<i>Arrhis_phyllonyx</i>	4 Benthos	Benthic	3	Peripheral
47	Ascidiacea_g_sp	4 Benthos	Benthic	6	Module connector
48	<i>Astarte_sp</i>	4 Benthos	Benthic	7	Peripheral
49	<i>Balanus_sp</i>	4 Benthos	Benthic	5	Peripheral
50	<i>Bathyarca_glacialis</i>	4 Benthos	Benthic	1	Peripheral
51	Bryozoa_indet	4 Benthos	Benthic	5	Peripheral
52	Benthos_larvae	4 Benthos	Benthopelagic	8	Module connector
53	<i>Buccinum_sp</i>	4 Benthos	Benthic	4	Peripheral
54	<i>Chaetozone_sp</i>	4 Benthos	Benthic	2	Peripheral
55	<i>Chionoecetes_opilio</i>	4 Benthos	Benthic	29	Peripheral
56	<i>Chlamys_islandica</i>	4 Benthos	Benthic	5	Peripheral
57	<i>Chone_sp</i>	4 Benthos	Benthic	4	Peripheral
58	<i>Ciona_intestinalis</i>	4 Benthos	Benthic	3	Peripheral
59	<i>Colus_sp</i>	4 Benthos	Benthic	2	Peripheral
60	<i>Crossaster_papposus</i>	4 Benthos	Benthic	5	Peripheral
61	<i>Ctenodiscus_crispatus</i>	4 Benthos	Benthic	3	Peripheral
62	<i>Electra_arctica</i>	4 Benthos	Benthic	4	Peripheral
63	Foraminifera	4 Benthos	Benthic	14	Module connector
64	<i>Galathowenia_sp</i>	4 Benthos	Benthic	3	Peripheral
65	Gammaridae_indet	4 Benthos	Benthic	19	Module connector
66	<i>Gonatus_fabricii</i>	4 Benthos	Pelagic	24	Peripheral
67	<i>Gorgonocephalus_sp</i>	4 Benthos	Benthic	2	Peripheral
68	<i>Heliometra_glacialis</i>	4 Benthos	Benthic	2	Peripheral
69	<i>Heteromastus_filiformis</i>	4 Benthos	Benthic	1	Peripheral
70	<i>Hyas_sp</i>	4 Benthos	Benthic	6	Peripheral
71	Hydrozoa_indet	4 Benthos	Benthic	2	Peripheral
72	<i>Maldane_sarsi</i>	4 Benthos	Benthic	3	Peripheral
73	<i>Mendicula_ferruginosa</i>	4 Benthos	Benthic	1	Peripheral
74	<i>Molpadia_borealis</i>	4 Benthos	Benthic	8	Peripheral
75	<i>Myriochele_herri</i>	4 Benthos	Benthic	2	Peripheral
76	<i>Nephtheidae_sp</i>	4 Benthos	Benthic	1	Peripheral
77	<i>Ophiacantha_bidentata</i>	4 Benthos	Benthic	8	Peripheral
78	<i>Ophiocten_sericeum</i>	4 Benthos	Benthic	4	Peripheral
79	<i>Ophiopholis_aculeata</i>	4 Benthos	Benthic	9	Peripheral
80	<i>Ophiopleura_borealis</i>	4 Benthos	Benthic	4	Peripheral
81	<i>Ophioscolex_glacialis</i>	4 Benthos	Benthic	2	Peripheral
82	<i>Ophiura_sp</i>	4 Benthos	Benthic	19	Peripheral
83	Ostracoda_indet	4 Benthos	Benthic	15	Module connector
84	<i>Pagurus_sp</i>	4 Benthos	Benthic	7	Peripheral
85	<i>Pandalus_borealis</i>	4 Benthos	Benthic	41	Module connector
86	<i>Paramphinome_jeffreysii</i>	4 Benthos	Benthic	2	Peripheral
87	<i>Phascolion_strombus</i>	4 Benthos	Benthic	3	Peripheral
88	Polychaeta	4 Benthos	Benthic	34	Module connector

89	<i>Polynoidae_indet</i>	4 Benthos	Benthic	17	Peripheral
90	<i>Pontaster_tenuispinus</i>	4 Benthos	Benthic	1	Peripheral
91	Porifera_g_sp	4 Benthos	Benthic	7	Peripheral
92	<i>Prionospio_cirrifera</i>	4 Benthos	Benthic	2	Peripheral
93	<i>Pycnogonida_g_sp</i>	4 Benthos	Benthic	7	Peripheral
94	<i>Rhachotropis_macropus</i>	4 Benthos	Benthic	5	Module connector
95	<i>Rossia_sp</i>	4 Benthos	Benthic	9	Module connector
96	<i>Sabinea_sp</i>	4 Benthos	Benthic	15	Module connector
97	<i>Scalibregma_inflatum</i>	4 Benthos	Benthic	5	Peripheral
98	<i>Sclerocrangon_ferox</i>	4 Benthos	Benthic	16	Peripheral
99	<i>Similipecten_greenlandicus</i>	4 Benthos	Benthic	4	Peripheral
100	<i>Spiochaetopterus_typicus</i>	4 Benthos	Benthic	7	Peripheral
101	<i>Spiophanes_kroeyeri</i>	4 Benthos	Benthic	2	Peripheral
102	<i>Spirorbidae_indet</i>	4 Benthos	Benthic	2	Peripheral
103	<i>Strongylocentrotus_sp</i>	4 Benthos	Benthic	7	Peripheral
104	<i>Terebellides_stroemi</i>	4 Benthos	Benthic	7	Module connector
105	<i>Thyasira_gouldi</i>	4 Benthos	Benthic	1	Peripheral
106	<i>Urasterias_linckii</i>	4 Benthos	Benthic	1	Peripheral
107	<i>Amblyraja_hyperborea</i>	5 Fish	Benthic	19	Peripheral
108	<i>Anarhichas_lupus</i>	5 Fish	Benthic	22	Module connector
109	<i>Anisarchus_medius</i>	5 Fish	Benthic	3	Peripheral
110	<i>Arctogadus_glacialis</i>	5 Fish	Pelagic	7	Peripheral
111	<i>Arctediellus_atlanticus</i>	5 Fish	Benthic	6	Peripheral
112	<i>Boreogadus_saida</i>	5 Fish	Benthic	42	Module connector
113	<i>Careproctus_sp</i>	5 Fish	Benthopelagic	8	Peripheral
114	<i>Cottunculus_microps</i>	5 Fish	Benthic	6	Peripheral
115	<i>Eumicrotremus_spinosus</i>	5 Fish	Benthic	8	Peripheral
116	<i>Gaidropsarus_argentatus</i>	5 Fish	Benthic	7	Peripheral
117	<i>Gymnelus_spp</i>	5 Fish	Benthic	7	Peripheral
118	<i>Gymnocanthus_tricuspis</i>	5 Fish	Benthic	8	Peripheral
119	<i>Hippoglossoides_platessoides</i>	5 Fish	Benthic	24	Module connector
120	<i>Icelus_spp</i>	5 Fish	Benthic	8	Module connector
121	<i>Leptagonus_decagonus</i>	5 Fish	Benthic	11	Module connector
122	<i>Leptoclinus_maculatus</i>	5 Fish	Benthic	2	Peripheral
123	<i>Liparis_fabricii</i>	5 Fish	Benthopelagic	7	Peripheral
124	<i>Liparis_gibbus</i>	5 Fish	Benthic	8	Peripheral
125	<i>Lumpenus_fabricii</i>	5 Fish	Benthic	4	Peripheral
126	<i>Lumpenus_lampraeformis</i>	5 Fish	Benthic	10	Module connector
127	<i>Lycenchelys_kolthoffi</i>	5 Fish	Benthic	2	Peripheral
128	<i>Lycodes_eudipleurostictus</i>	5 Fish	Benthic	7	Peripheral
129	<i>Lycodes_pallidus</i>	5 Fish	Benthic	17	Peripheral
130	<i>Lycodes_reticulatus</i>	5 Fish	Benthic	10	Peripheral
131	<i>Lycodes_rossi</i>	5 Fish	Benthic	4	Peripheral
132	<i>Lycodes_seminudus</i>	5 Fish	Benthic	9	Peripheral
133	<i>Mallotus_villosus</i>	5 Fish	Pelagic	36	Module hub
134	<i>Myoxocephalus_scorpis</i>	5 Fish	Benthic	5	Peripheral

135	<i>Paraliparis_bathybius</i>	5 Fish	Benthic	2	Peripheral
136	Fish_larvae	5 Fish	Benthopelagic	21	Module connector
137	<i>Reinhardtius_hippoglossoides</i>	5 Fish	Benthopelagic	23	Peripheral
138	<i>Triglops_murrayi</i>	5 Fish	Benthic	7	Peripheral
139	<i>Triglops_nybelini</i>	5 Fish	Benthic	4	Module connector
140	<i>Triglops_pingelii</i>	5 Fish	Benthic	10	Module connector
141	<i>Ulcina_olrikii</i>	5 Fish	Benthic	2	Peripheral
142	<i>Alle_alle</i>	6 Birds	Pelagic	26	Peripheral
143	<i>Fulmarus_glacialis</i>	6 Birds	Pelagic	20	Module connector
144	<i>Larus_hyperboreus</i>	6 Birds	Pelagic	3	Peripheral
145	<i>Rissa_tridactyla</i>	6 Birds	Pelagic	6	Peripheral
146	<i>Uria_lomvia</i>	6 Birds	Pelagic	2	Peripheral
147	<i>Balaenoptera_acutorostrata</i>	7 Mammals	Pelagic	13	Peripheral
148	<i>Balaenoptera_physalus</i>	7 Mammals	Pelagic	13	Peripheral
149	<i>Cystophora_cristata</i>	7 Mammals	Pelagic	13	Peripheral
150	<i>Delphinapterus_leucas</i>	7 Mammals	Pelagic	9	Peripheral
151	<i>Erignathus_barbatus</i>	7 Mammals	Benthic	30	Module connector
152	<i>Lagenorhynchus_albirostris</i>	7 Mammals	Pelagic	3	Peripheral
153	<i>Megaptera_novaeangliae</i>	7 Mammals	Pelagic	11	Peripheral
154	<i>Monodon_monoceros</i>	7 Mammals	Pelagic	7	Peripheral
155	<i>Odobenus_rosmarus</i>	7 Mammals	Benthic	15	Peripheral
156	<i>Orcinus_orca</i>	7 Mammals	Pelagic	6	Peripheral
157	<i>Pagophilus_groenlandicus</i>	7 Mammals	Benthopelagic	16	Peripheral
158	<i>Phoca_hispida</i>	7 Mammals	Benthopelagic	22	Module connector
159	<i>Ursus_maritimus</i>	7 Mammals	Benthopelagic	5	Peripheral

Table S3. Abbreviations, names and short definitions of food web metrics calculated in this paper.

Abbreviation	Full name	Definition	Reference
S	Species richness	Number of taxa (nodes) in a food web	Dunne (2009)
L	Trophic links	Number of trophic (feeding) interactions (links)	Dunne (2009)
LD	Link density	Mean number of links per species	Dunne (2009)
C	Connectance	Proportion of all possible links realized ($C=L/S^2$)	Dunne (2009)
% - Omni	Omnivores	Fraction of taxa that feed on resources on more than one trophic level	Petchey (2008)
% - Can	Cannibals	Fraction of taxa that feed on themselves	
% in loops	Species in loops	Fraction of taxa that occur in loops. A loop describes a pathway of interactions from a certain species without visiting the species more than once	Williams (2010)
MeanPath	Mean shortest path length	Mean shortest path of feeding links connecting each pair of taxa in a food web	Dunne (2009)
MeanOmni	Mean level of omnivory	Level of omnivory of each species is the standard deviation of the SWTL of its resources.	Petchey (2008)
MeanSWTL	Mean short-weighted Trophic level	Mean of all short weighted paths + 1 from base to each species of interest	Williams & Martinez (2004)
MeanClust	Mean clustering	The probability that two neighbours of a species are neighbours themselves	Girvan & Newman (2002)
Mod	Modularity	Modularity refers to subgroups of species interacting more with each other than with species from other subgroups	Newman & Girvan (2004)

References: Dunne, J. A. 2009 Food webs. In Complex Networks and Graph Theory section of the Encyclopedia of Complexity and Systems Science, pp. 3661–3682. Ed. by R. A. Meyers. Springer, New York.; Petchey, O. L., Beckerman, A.P., Riede, J.O, Warren, P.H. 2008 Size, foraging and food web structure. *PNAS*. **100**, 614-622; Williams, R. 2010 Network 3D software. *Microsoft Research, Cambridge, UK*; Williams R. J., Martinez, N. D. 2004 Limits to trophic levels and omnivory in complex food webs: theory and data. *Am Nat.* 163, 458-468; Girvan, M., Newman, M. E. J. 2002 Community structure in social and biological networks *Proc. Natl. Acad. Sci.* **90**, 7821-7826; Newman, M. E., Girvan, M. 2004 Finding and evaluating community structure in networks. *Phys. Rev. E.* **69**, 026113.

Table S4. List of 51 fish taxa (in alphabetical order) used to calculate the degree centrality maps. For some fish the occurrence data at station level had a lower taxonomic resolution (e.g. *Zoarcidae* family rather than genus and species level) than in the food web matrix meta-web. For these taxa, we calculated the mean degree centrality of the taxonomic level of interest (e.g. family) based on the degree centrality of the member species.

Amblyraja hyperborea, *Amblyraja radiata*, *Anarhichas denticulatus*, *Anarhichas lupus*, *Anarhichas minor*, *Anisarchus medius*, *Argentina* sp, *Artediellus atlanticus*, *Bathyraja spinicauda*, *Brosme brosme*, *Careproctus* sp., *Cottunculus microps*, *Cyclopterus lumpus*, *Enchelyopus cimbrius*, *Eumicrotremus spinosus*, *Gadiculus argenteus*, *Gadus morhua*, *Gaidropsarus argentatus*, *Glyptocephalus cynoglossus*, *Gymnocanthus tricuspis*, *Hippoglossus hippoglossus*, *Hippoglossoides platessoides*, *Icelus* spp., *Leptagonus decagonus*, *Leptoclinus maculatus*, *Limanda limanda*, *Liparis montagui*, *Lumpenus fabricii*, *Lumpenus lampraeformis*, *Lycodes esmarkii*, *Lycodes gracilis*, *Macrourus berglax*, *Melanogrammus aeglefinus*, *Merlangius merlangus*, *Microstomus kitt*, *Micromesistius poutassou*, *Molva molva*, *Myoxocephalus Scorpius*, *Pleuronectes platessa*, *Pollachius virens*, *Rajella fyllae*, *Reinhardtius hippoglossoides*, *Sebastes mentella*, *Sebastes* spp., *Sebastes viviparous*, *Triglops murrayi*, *Triglops nybelini*, *Triglops pingelii*, *Trisopterus esmarkii*, *Ulcina olrikii*, *Zoarcidae* (include these taxa: *Gymnelus* spp., *Lycodes eudipleurostictus*, *Lycodes pallidus*, *Lycodes reticulatus*, *Lycodes rossi*, *Lycodes seminudus*)

