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Faculty of of Biosciences, Fisheries, and Economics

Effect of climate change and invasive species on Arctic marine food-webs

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Abstract

Climate warming induces poleward distributional shifts of boreal species in Arctic regions resulting in compositional changes with poorly understood consequences for Arctic food-webs. This thesis addresses the spatial variation in Barents Sea food-webs using previously compiled distributional data in polygons specified for the Nowegian and Barents Sea NoBa Atlantis model and a highly resolved Barents Sea metaweb dataset. Further, it studies implications of cod and snow crab invasion for Arctic marine food-webs organization. Spatial overlap across NoBa polygons was estimated for all pairs of interacting species in the metaweb and used as link weight for the metaweb to investigate zoogeographic patterns. Food-webs were compiled for the NoBa polygons based on compositional and metaweb data to address the spatial variation in food-web structure. For each food-web, a set of standard structural properties affecting food-web ecology was estimated. Environmental data and community weighted means of traits available for the species in the metaweb were compiled for each NoBa polygon to support analysis of spatial variation. The environmental, compositional, traits and food-web structure data were analysed by multivariate methods to map and assess spatial variation across NoBa polygons. Despite gradual change in environmental, compositional and traits characteristics along the ocean climate gradient separating Atlantic from Arctic regions, food-web organization displayed a discontinuity with a strong structural difference between the three Arctic polygons and the remaining food-webs. The structural difference concerned primarily food-web connectance, modularity and degree of omnivory, three properties that distinguish Arctic from Atlantic food-webs. Addition of cod to the three Arctic food-webs shortened path lengths connecting species, and strongly modified food-web structure, reducing modularity and increasing connectance and omnivory, thereby increasing their similarity to Atlantic food-webs. The addition of snow crab to Arctic polygons had a similar but far less pronounced effect due to its lower degree of generalism relative to cod and nearly exclusive affiliation with the benthic food-web compartment. The strong structural change in Arctic food-webs imposed by climate-driven cod invasion goes in the direction of reduced robustness against environmental perturbations. A reduced food-web robustness is concerning considering the likelihood of increased environmental perturbations in the Arctic due to higher climate variability and expanding human activities driven by climate change.

Keywords: biogeography, Barents Sea, Arctic, marine food-web, invasion.

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1 INTRODUCTION

Arctic marine food-webs are shaped by the environmental conditions found in Arctic waters (Dalpapado et al., 2014; Kortsch et al., 2019; Ingvaldsen et al., 2021; Wassman et al., 2021). Low water temperatures and sea-ice cover are characteristic environmental conditions that influence species composition and ecosystem compartments in Arctic water masses. The light availability influenced by sea-ice formation and melting and by the sharp seasonality in photoperiod cause strong seasonal variation in productivity. When the spring comes and the days gain in length there is a bloom of primary production (Lovvorn et al., 2005; Bluhm et al., 2015; Ingvaldsen et al., 2021). The algal bloom is not grazed down by zooplankton, which after a winter below the sea ice has a low biomass. Thereby the organic matter sinks to the bottom, and on the shallow continental shelves it is used by the benthos (Wassman et al., 2021). Pelagic production and sedimentation are very different under open water conditions experienced further South, where there is greater light availability and the zooplankton can graze on the spring bloom immediately, resulting in an important pelagic production and reduced amount of carbon that reaches the bottom (Schmoker et al., 2013). Thereby, Arctic food-webs have a diverse benthic compartment, and a pelagic compartment that is less prominent than in more temperate and productive ecosystems (Ingvaldsen et al., 2021). The environmental and compositional differences between Arctic and more southerly ecosystems result in structurally different food-webs (Kortsch et al., 2019; Pecuchet et al., 2022). Arctic food-webs are being rewired by climate-driven range shifts, local extinctions, and invasions, causing change in spatial food-web variability at the zoogeographic scale (Kortsch et al., 2015; Ingvaldsen et al., 2019; Pecuchet et al., 2020).

The Arctic is experiencing warming due to climate change at a higher rate than anywhere else in the world, with temperatures rising at more than twice the global average (McBean et al., 2005; Anisimov et al., 2007; IPCC, 2014). In Arctic regions influenced by Atlantic water masses the inflow of Atlantic water is increasing (Lind et al., 2016; Ingvaldsen et al., 2021). This higher inflow of Atlantic water increases the salinity of the water column, reducing stratification and potentially altering nutrient fluxes and primary production (Lind et al., 2016; Polyakov et al., 2020). The combined effect of warmer atmospheric temperatures and water have a synergistic effect in sea-ice loss (Olonscheck et al., 2019), which in turn translates into habitat loss for sea-ice associated species. Currently, climate driven environmental change is having a great impact on marine species distributions worldwide (Walther et al, 2002; Doney et al., 2012; Bogstad et al., 2015; Lotze et al., 2019; Cooley et al., 2022). In the Arctic, the species that are redistributing include amphipods, polar cod (*Boreogadus saida*) and sea mammals such as seals and polar bears (Blanchet et al., 2019). Ice-loss is leading to increases in primary production and a greater importance of the pelagic compartment in the Arctic (Dalpapado et al., 2020; Ingvaldsen et al., 2021). The climate driven environmental change is detrimental to many Arctic species, but advantageous to boreal species. Therefore, boreal species are expanding their distribution in the Arctic, a phenomenon known as borealization (Dalpapado et al., 2012; Fossheim et al., 2015; Dalpapado et al., 2020; Frainer et al., 2021).

Rapid poleward distributional shifts driven by climate warming have been observed in the Arctic (Fossheim et al., 2015; Mueter et al., 2021). Among the species displaying the most rapid shifts are mobile, often migratory, species such as fish, sea birds and sea mammals (Ingvaldsen et al. 2021). During the last few decades of warming, boreal fish species have rapidly colonized Arctic waters changing the composition of Arctic fish communities (Fossheim et al., 2015; Frainer et al., 2017; Mueter et al., 2021; Frainer et al., 2021; Emblemsvåg et al., 2022a). The borealization process affects functional traits composition of communities and food-web organization in the Arctic (Wiedmann et al., 2014; Kortsch et al. 2015; Frainer et al., 2017). This is due to zoogeographic differences in traits composition, with Arctic fish species being small, specialized benthivores, and boreal species being large, semi-pelagic generalists (Frainer et al., 2017; Ingvaldsen et al., 2021). The boreal species redistributions result in new feeding links rewiring Arctic food-webs, as observed in the Barents Sea (Kortsch et al., 2015; Pecuchet et al., 2020).

The Barents Sea is a high latitude ecosystem influenced by Arctic and Atlantic water masses meeting along the polar front (Parsons et al., 1996; Ozhigin et al., 2011; Ingvaldsen et al., 2021). The frontal area of the Barents Sea acts as a biogeographic transition zone that is strongly affected by climate change. The Arctic and Atlantic water masses define distinct environmental conditions associated with different species compositions and functional characteristics (Frainer et al., 2017; Pecuchet et al., 2022). The resulting biogeographic differences in feeding links are a main source of spatial variability in food-web structure (Kortsch et al., 2015; Kortsch et al., 2019; Pecuchet et al., 2020). Climate change is causing a reconfiguration of Barents Sea environmental conditions and species composition, with boreal species moving to higher latitudes, and Arctic species being displaced or finding new challenges in their environment and ecological interactions. The environmental and compositional change is spatially heterogeneous, and the food-web implications depend on the structure of the recipient food-web and the traits of incoming species (Kortsch et al., 2015; Frainer et al., 2017; Pecuchet et al., 2020).

This study aims to shed light on the spatial ecology of Arctic marine food-webs, and the implications of climate-driven redistributions and invasions for Arctic food-web structure. The three main objectives of the thesis are to:

i. study the spatial overlap between interacting trophospecies and the zoogeography of co-occurrence;
ii. investigate drivers of spatial variability in the food-web;
iii. assess change in Arctic food-web structure due to poleward redistribution and invasion.

To address the above objectives, I studied the spatial variability in environmental conditions, species composition, traits, and food-web configuration across 25 areas in the Barents Sea. Further, I investigated the effects on food-web structure of colonization of Arctic areas by the incoming, generalist species Atlantic cod (*Gadus morhua*) and snow crab (*Chionoecetes opilio*).

The main hypotheses of the study are: i) the zoogeographic divide affects species co-occurrences and feeding links in the Barents Sea; ii) differences in feeding behaviour between the Arctic and boreal species have structural implications for food-webs, with Arctic food-webs having lower connectance and lower degree of omnivory; and iii) the species' redistribution and invasion will reorganize the Arctic food-web into a more boreal one.

2 MATERIALS AND METHODS

2.1 Area of study

The Barents Sea is one of the high latitude ecosystems surrounding the Polar Basin. It covers an area of ~1.6 million km^2 with an average depth of 230 m and a maximum depth of 500 m (Ozhigin et al., 2011). There are three main water masses in the Barents Sea: Coastal Water, Atlantic Water and Arctic Water (Loeng, 1991). Warm Atlantic waters enter the area from the South towards the central and North Barents Sea, while the North and North-East Barents Sea has traditionally been dominated by the influence of an Arctic Water inflow and a seasonal cover of sea-ice (Figure 1; Helland-Hansen & Nansen, 1909; Ådlandsvik & Loeng, 1991; Loeng & Sætre, 2001; Lind et al., 2016). The last decades have seen an increase in the influence of Atlantic water in the Arctic Barents Sea, a phenomenon known as atlantification, with a steady increase in sea water temperature, and a decrease in the amount and duration of sea-ice cover (Ingvaldsen et al., 2021). The area of mixed waters around the polar front in the central Barents Sea has expanded (Fossheim et al. 2015; Ingvaldsen et al., 2021).

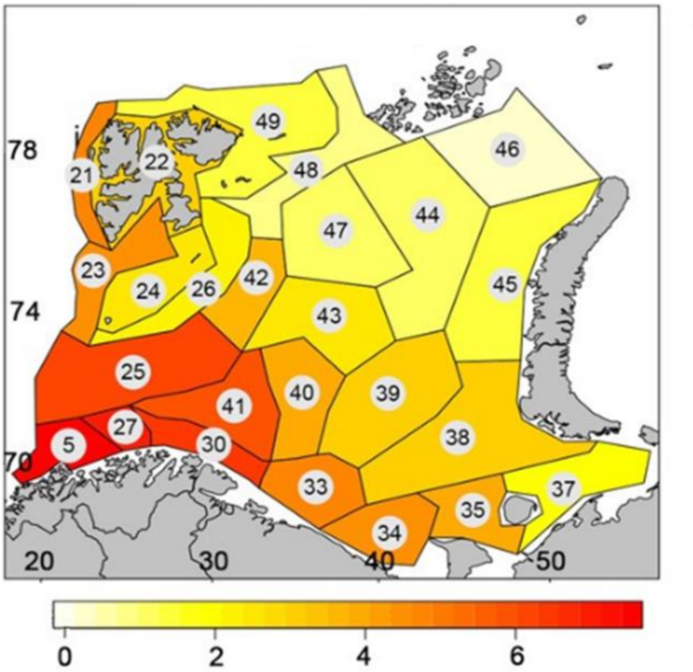


Figure 1. Barents Sea map and Atlantis polygons. Mean water column temperature in the polygons shows the Arctic versus Atlantic water masses (red, warm Atlantic water; yellow, cold Arctic water- from Kortsch et al., 2019).

The Barents Sea study area was divided into 25 subregions coinciding with the NoBa Atlantis model polygons (Hansen et al., 2016). The spatial configuration of the polygons emphasises homogeneous hydrography and bathymetry.

2.2 Environmental data

The environmental data included in the analyses of spatial variation across NoBa polygons were the polygons' mean water temperature (ºC), mean salinity (PSU), mean depth (m), and mean number of days per year with sea-ice cover (Table S1). The water temperature and salinity data from 2004 to 2007 were obtained from the Conductivity-Temperature-Depth (CTD) profiles taken annually in August and September during the joint Norwegian-Russian Barents Sea ecosystem survey conducted by the Institute of Marine Research and the Knipovich Polar Research Institute of Marine Fisheries and Oceanography. The depth data were also obtained from the Barents Sea ecosystem survey. The sea-ice data were obtained from the National Snow and Ice Data Centre and are based on satellite imagery (Kortsch et al., 2019). The total number of days per year with more than 15% of sea-ice concentration was averaged for each polygon over the period 2004 to 2007 (for further details see Kortsch et al., 2019).

2.3 Biological data

Biological data encompassed compositional, traits and feeding links information for 233 trophospecies, i.e., taxa sharing the same predators and prey, found in the Barents Sea (Kortsch et al., 2019). The trophospecies were affiliated with 6 functional groups, with 10 basal (primary producers), 43 zooplankton, 79 benthic, 77 fish, 9 sea-bird, and 15 marine mammal taxa.

The *compositional data* for the NoBa polygons were obtained from Kortsch et al. (2019), who provided a compilation based on the joint Russian–Norwegian Barents Sea Ecosystem Survey and expert knowledge elicitation, referring to conditions in the Barents Sea prior to 2006. The distributional data from the Barents Sea Ecosystem Survey, which samples in August/September, reflect the summer distribution of species, many of which are seasonal migrants. Snow crab was removed from the baseline compositional data in Kortsch et al. (2019), as this invasive species entered the Barents Sea in later years. The resulting data are here forth referred to as the original trophospecies compositions across NoBa polygons, i.e., before climate driven changes in distribution and snow crab invasion.

The *traits data* used to compile the community weighted mean (CWM) trait table for the NoBa polygons were obtained from Pecuchet et al. (2020) or derived from food-web data (Table S2). The traits data include body length (cm), feeding mode (suspension feeder, deposit feeder, predator), habitat use (benthic, bentho-pelagic, pelagic), trophic level (obtained from the metaweb), degree of omnivory (obtained from the metaweb), generalism (number of prey in the metaweb), and vulnerability (number of predators in the metaweb). The traits were selected based on their potential influence on feeding links and food-web structure.

The *food-web data* for the NoBa polygons were derived from a Barents Sea metaweb (Kortsch et al., 2019). The metaweb contains 233 trophospecies and 2218 feeding links. Food-webs were constructed for each of the 25 polygons based on the metaweb and on trophospecies compositional information. The compositional data were used to sub-set the metaweb adjacency matrix to obtain the polygon specific food-web adjacency matrix.

The food-web adjacency matrices of the NoBa polygons were used to compute a selection of *food-web metrics*, based on Dunne (2009) and following Kortsch et al. (2019), that capture important structural properties with ecological implications. The metrics chosen to address topological food-web properties were: 1) number of species (S); 2) number of links (L); 3) link density (LD); 4) connectance (C); 5) clustering (Clust); 6) modularity (Comp); 7) degree of omnivory (Omni); 8) predator per prey (PredPrey); 9) proportion of cannibals (Can); 10) proportion of basal species (Bas); 11) proportion of top species (Top); 12) proportion of intermediate species (Int); 13) generality SD (GenSD); 14) vulnerability SD (VulSD); 15) mean short-weighted (sw) trophic level (meanSWTL); 16) mean shortest path length (meanPath). The food-web metrics for each NoBa polygon were computed and used to compile a food-web metrics table for further analyses (Table S3). An explanation of the food-web metrics and their structural and dynamical implications can be found in the appendix (Table S4).

2.4 Data analysis

2.4.1 Trophospecies co-occurrence and spatial overlap

To inspect the influence of zoogeography on spatial overlap and food-web wiring, two measures of spatial overlap for interacting species were calculated based on co-occurrence information. The frequency of co-occurrence across all polygons in the Barents Sea was calculated as the proportion of polygons where two species co-occurred out of the 25 polygons. The spatial overlap, accounting for spatial extent of trophospecies' distributions, was calculated as the proportion of polygons in which two species co-occurred out of the number of polygons in which they were found. Diagrams displaying spatial overlap among trophospecies were produced for the unweighted metaweb and for the metaweb with links weighted by degree of spatial overlap. Nodes showing functional group (colour coded) and either zoogeographic or module affiliation (coded as different symbols) were included in the diagrams. Module affiliation was assigned to trophospecies based on the outcomes of a spinglass modularity analysis applied to the metaweb with links weighted by degree of spatial overlap.

2.4.2 Spatial variation in community structure

The variation across polygons in environmental, compositional, community weighted mean traits and food-web structural properties was analysed by multivariate methods. To quantify the multidimensional variation across polygons, distance metrics were computed for each set of environmental and biological data. Euclidean distance was applied to the scaled environmental, CWM traits and food-web metrics data, as these datasets consist of continuous variables (Greenacre and Primicerio 2014). For the compositional data the Jaccard distance was used, as it is appropriate for binary, presence-absence data. Based on the distance matrices, hierarchical clustering (with complete linkage) and Multidimensional Scaling (MDS) were computed to summarize the spatial variation via dendrograms and multidimensional maps. Principal Components Analysis (PCA) was applied to the environmental and food-web metrics data to visualize the response variables in the corresponding biplots. The MDS maps and PCA biplots share the same coordinates for the sampled NoBa polygons. The distance matrices were correlated to inspect the relationships between polygons' variation in environmental and biological characteristics and assess whether small differences between polygons and gradual change in environmental conditions, composition or CWM traits correspond to small differences and gradual change in food-web structure.

2.4.3 Reconfiguration of food-web structure

To address the effects of incoming species on food-web structure, the trophospecies composition of the polygons was modified to account for colonization by the generalists Atlantic cod (Townhill et al., 2021), hereon referred as cod, and snow crab (Zakharov et al., 2021). The number of prey and predators of cod and snow crab in each functional group of the Barents Sea metaweb can be found in Table 1. Following the introduction of new species, the food-web metrics tables and the associated distance matrices were computed to calculate the MDS that summarize food-web structural changes.

The effects of new species introductions on path lengths connecting trophospecies in the food-webs was addressed by contrasting the shortest path lengths in the reference Arctic food-webs in NoBa polygons 44, 45, and 46, with shortest path lengths obtained after the introduction in those polygons of either cod, snow-crab, or both species.

Table 1. Number of feeding links of snow crab and cod with other trophospecies in the Barents Sea metaweb.

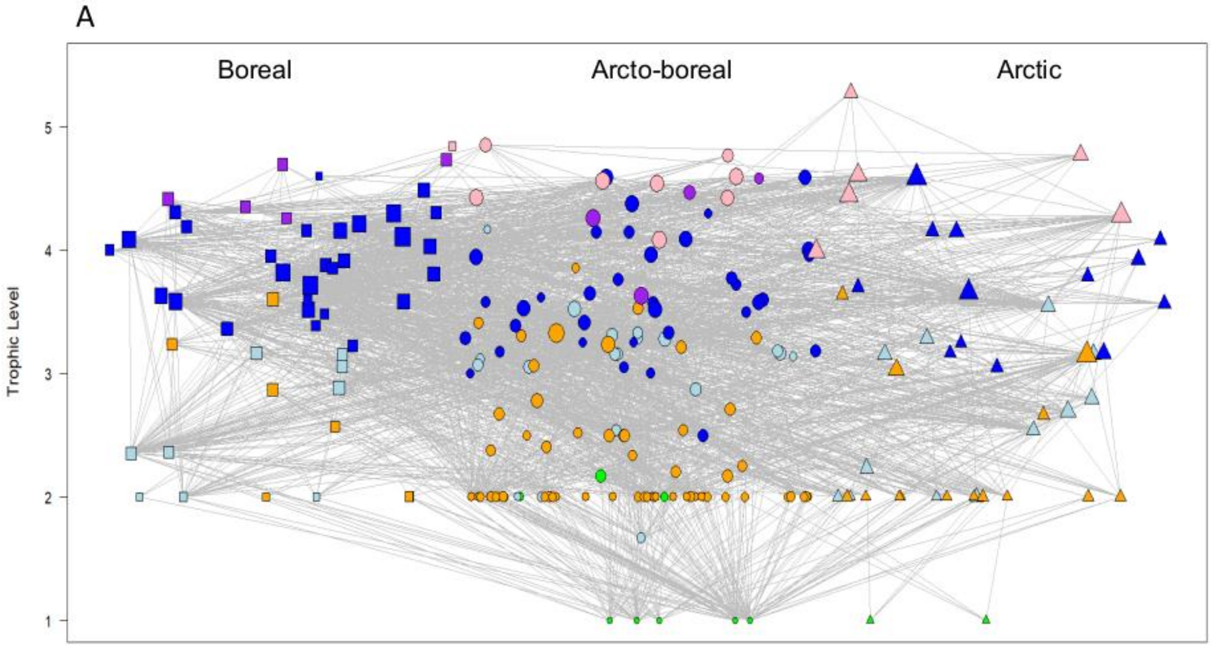
		ZOOPLANKTON	**BENTHOS**	**FISH**	**SEABIRDS**	**MAMMALS**
SNOW CRAB	*Prey*	3	24	2	-	-
	Predator	-	2	2	-	-
COD	*Prey*	19	32	52	-	-
	Predator	-	-	18	6	11

All analyses and graphic output were done in R version 4.2.2, “Innocent and Trusting” (R core Team, 2022). The MDS analyses were carried out using the «vegan» package (Oksanen et al., 2022). The “igraph” package (Csardi & Nepusz, 2006) was used for the network analysis and plotting, and the “NetIndices” package (Kones et al., 2009) was used to calculate network indices, including trophic level and degree of omnivory.

3 RESULTS

3.1 Spatial overlap and metaweb modularity

The zoogeographic separation of species in the Barents Sea metaweb (Figure 2A) is reflected in the degree of spatial overlap between interacting trophospecies, as seen in the graphic representation of the Barents Sea metaweb, with link weights expressing spatial overlap between trophospecies (Figure 2B). A few Arctic trophospecies (*Somniosus microcephalus*, *Boreogadus saida*, *Erignatus barbatus*, *Pandalus borealis*) show high spatial overlap with boreal or Arcto-boreal trophospecies (Figure 2B). Five modules were identified in the weighted metaweb by the spinglass algorithm (Figure 2B). The modules consist of benthic vs pelagic compartment, and low vs high trophic levels, and do not clearly distinguish Arctic and boreal trophospecies at this coarse resolution.



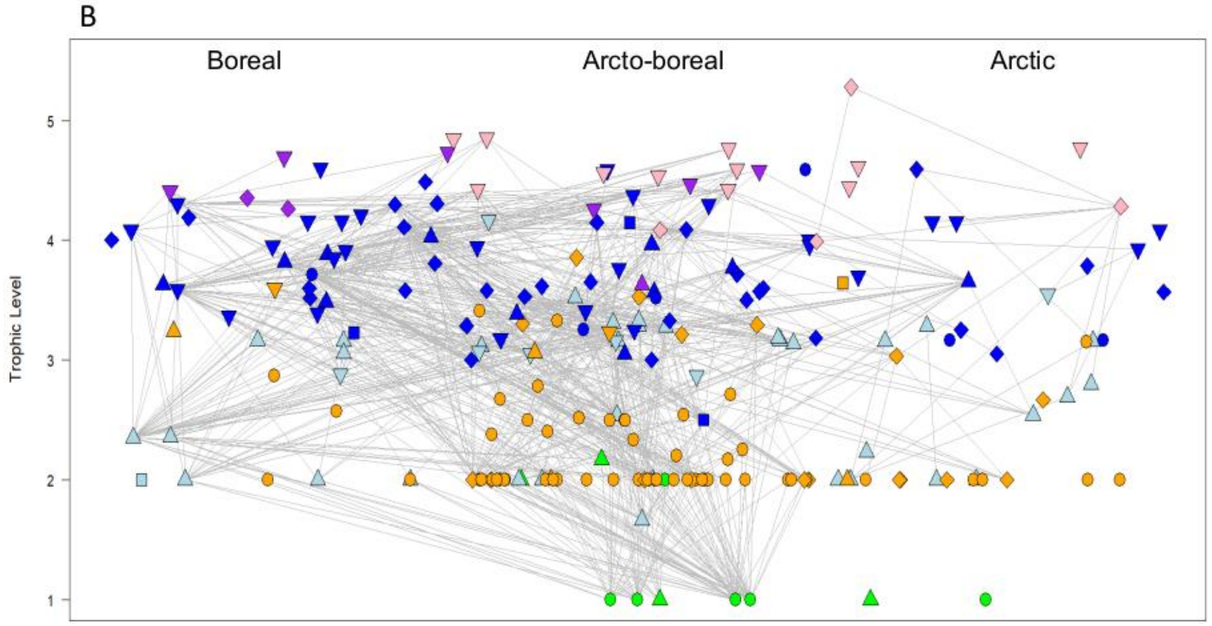


Figure 2. Barents Sea metaweb. The symbols represent trophospecies, which are distributed from left to right according to biogeographic affiliation, and vertically according to trophic level. The colours code for the 6 functional groups (green, phytoplankton; light blue, zooplankton; orange, benthos; blue, fish; purple, sea birds; light pink, mammals). A) Barents Sea metaweb topology. The symbols represent zoogeographic affiliation (rectangles, boreal trophospecies; circles, Arcto-boreal trophospecies; triangles, Arctic trophospecies), and the size of the symbols is proportional to the number of prey of trophospecies. B) Barents Sea metaweb with links weighted by spatial overlap between interacting trophospecies. Only the links between trophospecies that spatially overlap more than 60% are represented. The symbols indicate module affiliation, with five modules detected by the spinglass modularity algorithm.

3.2 Spatial variation in community structure

The strongest environmental gradient, captured by the first ordination axis of the PCA and MDS, accounts for ocean climate, separating Atlantic vs Arctic regions that display different water temperatures and sea-ice conditions (Figure 3,4A). The second ordination axis accounts for a depth gradient. The first two principal components of the environmental conditions account for 87.5% of the variation, with the first principal component of ocean climate accounting for 55.2% of the variation (Figure 3, Table S5).

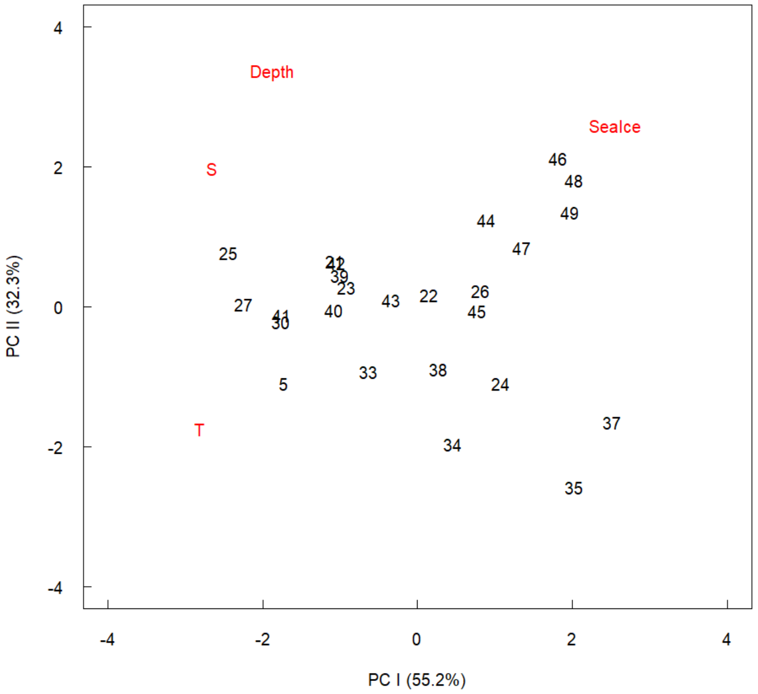


Figure 3. Biplot of PCA results for the environmental characteristics of the NoBa polygons (black labels). The abbreviations of environmental variables (in red) associated with the factor loadings are: T, mean temperature; S, mean salinity; Depth, mean depth; SeaIce, mean days of sea-ice cover per year.

The ocean climate gradient (Figure 4A) aligned with the main MDS gradient of community structure (Figure 4B), is associated with the boreal vs Arctic compositional divide. The MDS map based on traits is not aligned with the main environmental or compositional gradients of variation but does show a separation between Arctic and other polygons (Figure 4C). The MDS map of food-web metrics shows a clear separation between three Arctic polygons (44, 45, 46) and the other NoBa polygons along the main axis of variation. The strong separation between the three Arctic polygons and the other polygons is not observed in the environmental, compositional or traits data (Figure 4D, 7A). The main gradient of food-web structure, accounting for 63.3% of variation, concerns food-web metrics modularity and connectance (Figure 7A, Table S6). Modularity is, on average, 24.9% higher in the Arctic polygons compared to the others, and connectance and degree of omnivory are lower in the Arctic polygons (Figure 7A, Table S3).

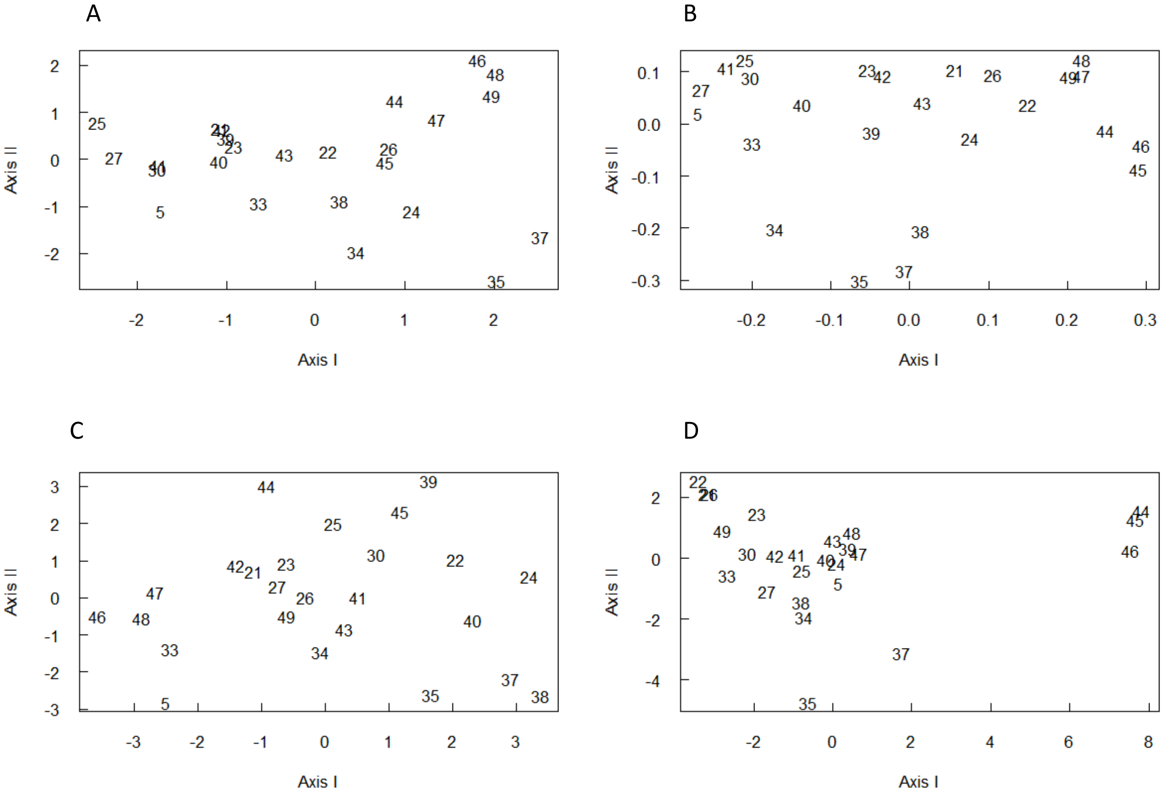


Figure 4. MDS maps for NoBa polygons. A) Environmental conditions, B) trophospecies composition, C) community weighted mean traits, and D) food-web metrics. The NoBa polygon numbers label the samples.

The hierarchical clustering results show a clear separation between Arctic and Atlantic polygons for environmental conditions and compositional data (Figure 5A, B). For the CWM traits data, the clustering is less distinctively related to geographic position, with one cluster being composed of both Arctic and Atlantic polygons (Figure 5C). For the food-web metrics, there is a clear separation of the three Arctic polygons in North-East from other Arctic or Atlantic polygons (Figure 5D).

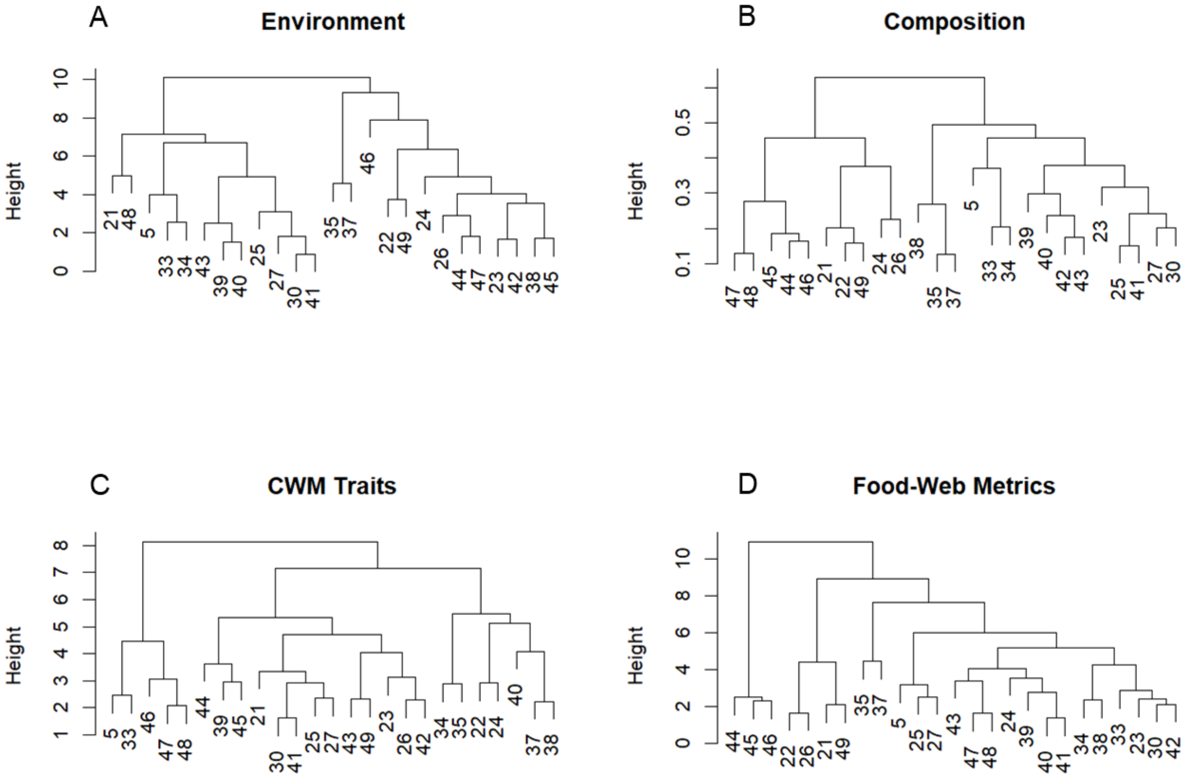


Figure 5. Dendrograms of hierarchical clustering results for NoBa polygons. A) Environmental conditions; B) trophospecies composition; C) community weighted mean traits; and D) food-web metrics. The leaves of the dendrograms are labelled by the corresponding NoBa polygon numbers.

The correlation between distance matrices shows a linear relationship between environmental and compositional distances and between compositional and traits distances (Figure 6A, B, respectively). This is not the case in the relationships with the food-web metrics distances; for small to intermediate distances between polygons in compositional or traits data there can be small or large differences in food-web metrics (Figure 6C, D). The large differences in food-web structure concern comparisons between the three Arctic polygons (44, 45, 46) and other polygons that are similar compositionally or with regards to traits.

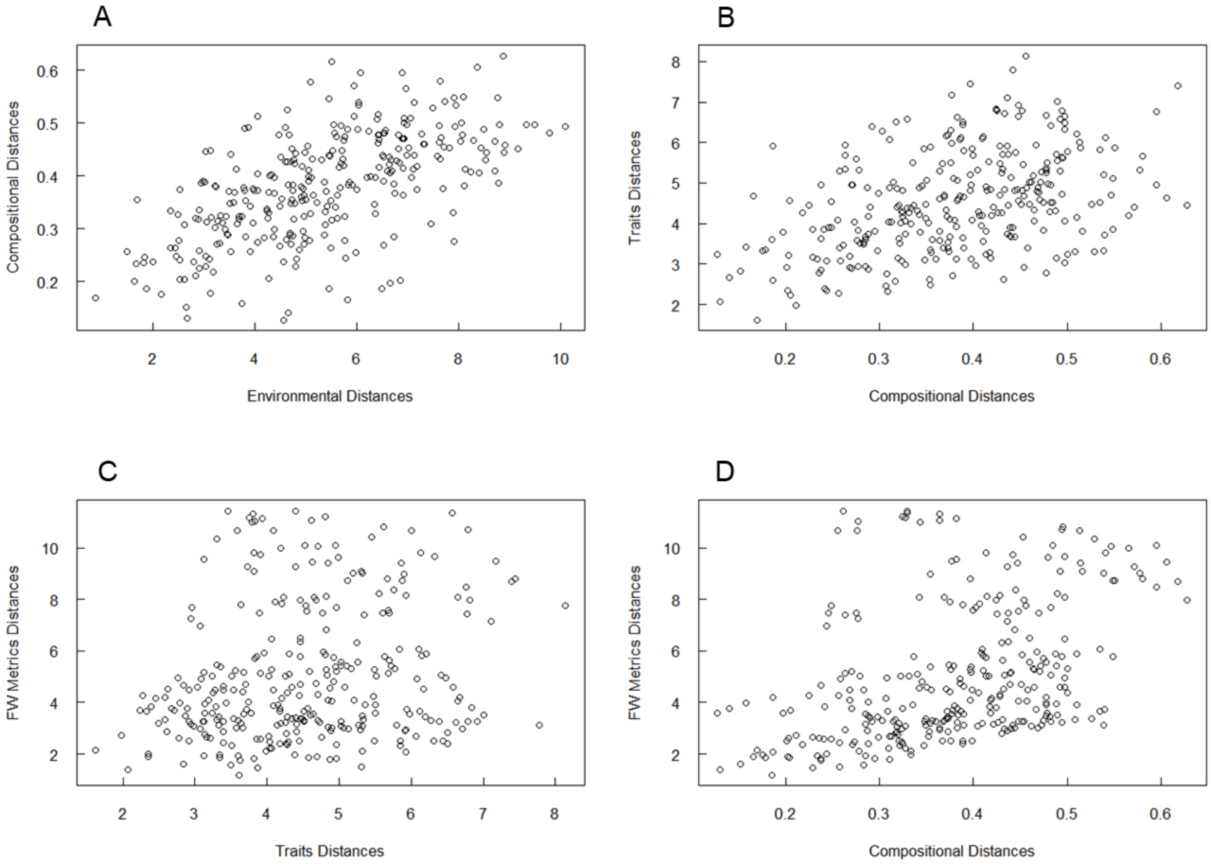


Figure 6. Scatter plots of the relationships between distance matrices for the NoBa polygons. A) environmental vs compositional distances; B) compositional vs traits distances; C) traits vs food-web metrics distances; and D) compositional vs food-web metrics distances.

3.3 Reconfiguration of food-web structure

The first principal component of the PCA on food-web metrics, which separates the three Arctic polygons from the rest, is positively related to modularity, and negatively related to connectance, generalism, and degree of omnivory (Figure 7A, Table S6). After the introduction of cod (Figure 7B), the Arctic polygons (44, 45 and 46) substantially reduced their distance from the rest of the polygons. Modularity of the Arctic polygons was reduced, on average, by 7.3%, whereas connectance and degree of omnivory increased 11.3% and 1.6%, respectively (Table 2). After the introduction of snow crab (Figure 7C), the Arctic polygons reduced their distance from the other polygons along the first ordination axis, but to a much lesser degree than when cod was introduced. Modularity was reduced by 1.2%, and connectance and degree of omnivory increased by 3.1% and 1.0%, respectively (Table 2). When snow crab and cod were introduced together, the effect on food-web metrics of the

Arctic polygons was similar but greater than the effect of the cod introduction, showing an additive effect of cod and snow crab on food-web structure (Figure 7D). The modularity of the Arctic polygons was reduced by 8.6%. Connectance increased by 13.4%, and degree of omnivory by 2.8% (Table 2).

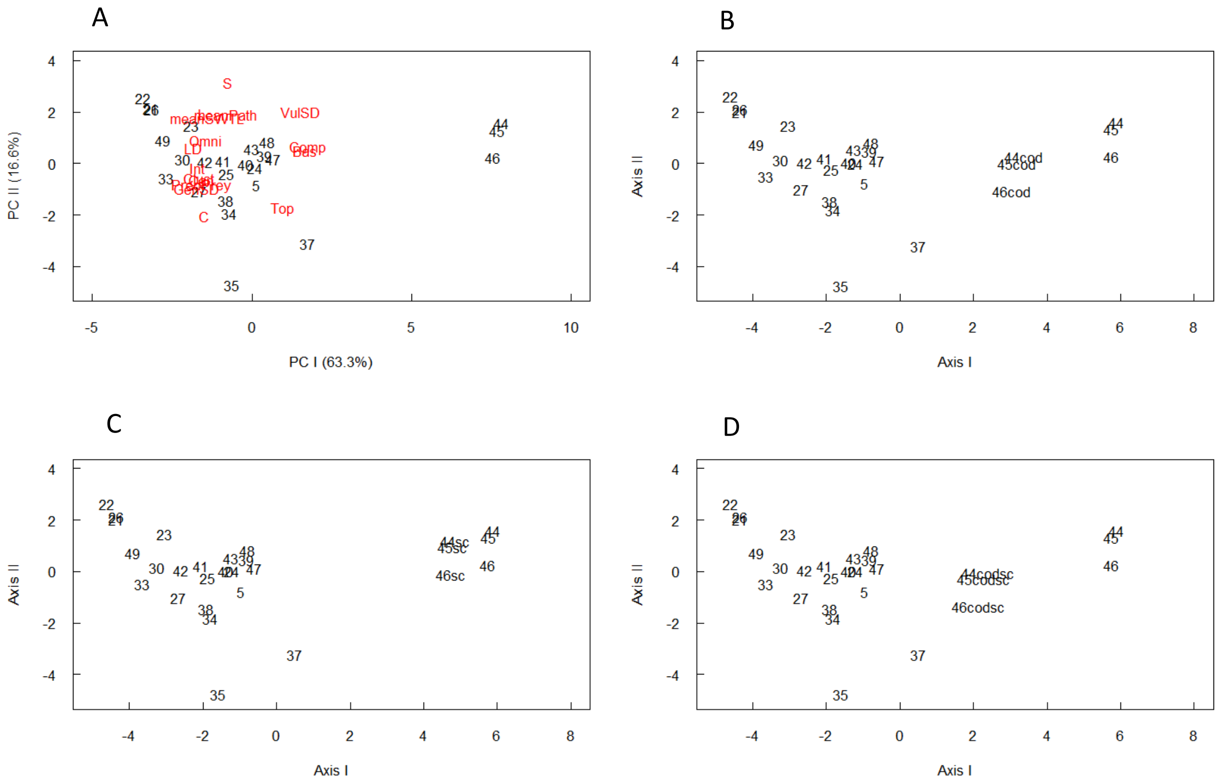


Figure 7. Ordination maps of food-web structure across NoBa polygons before and after the introduction of cod and/or snow crab in the Arctic NoBa polygons (polygon nr 44, 45, 46). A) Biplot of the PCA results of the food-web metrics for the original trophospecies compositions. B) MDS map with Arctic polygons excluding (44, 45, 46) and including cod (44cod, 45cod and 46cod). C) MDS map with Arctic polygons excluding (44, 45, 46) and including snow crab (44sc, 45sc and 46sc). D) MDS map with Arctic polygons excluding (44,45,46) and including cod and snow crab (44codsc, 45codsc and 46codsc).

Table 2. Selection of food-web metrics of the Arctic NoBa polygons before and after introduction of cod and/or snow crab. The metrics are connectance (C), modularity (Comp), degree of omnivory (Omni), mean shortest path length (meanPath). Polygon labels indicate food-webs without cod or snow crab (44, 45, 46), with cod (COD), with snow crab (SC) and with both species (CODSC).

POLYGON	C	COMP	OMNI	MEANPATH
44	0.032	0.369	0.178	2.119
45	0.031	0.352	0.154	2.091
46	0.034	0.347	0.170	2.023
44COD	0.036	0.340	0.180	2.060
45COD	0.034	0.327	0.156	2.053
46COD	0.038	0.323	0.174	2.007
44SC	0.033	0.361	0.180	2.112
45SC	0.032	0.351	0.155	2.085
46SC	0.035	0.343	0.172	2.020
44CODSC	0.036	0.331	0.182	2.075
45CODSC	0.035	0.324	0.158	2.067
46CODSC	0.039	0.321	0.176	2.021

The introduction of cod substantially reduced path lengths between pairs of trophospecies in the Arctic food-webs (Figure 8). A similar but less pronounced effect can be seen after the introduction of snow crab (Table S7). The introduction of both species has the greatest effect on shortest path lengths (Figure 8).

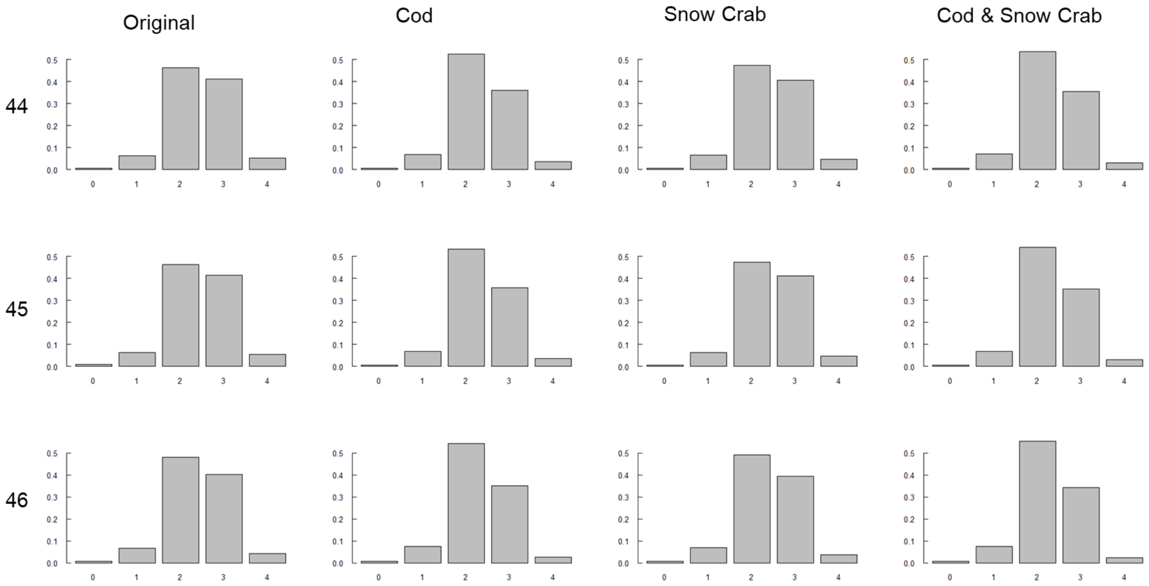


Figure 8. Histograms of shortest path length frequency distribution in the Arctic polygons (44, 45 and 46). From left to right: original trophospecies composition; with cod; with snow crab; and with both species.

4 DISCUSSION

The results show clear spatial patterns in the Barents Sea food-webs related to ocean climate and zoogeography. The zoogeographic divide affects trophospecies co-occurrences, and thereby the likelihood of feeding interactions in the Arctic vs Atlantic water masses, with only a few Arctic species presenting high overlap with boreal species. The boreal and Arcto-boreal species have many feeding links with high spatial overlap between the species involved. The Arctic species have fewer feeding links, primarily within the benthic compartment, contributing to a more sparsely connected food-web. The ocean climate gradient from the South-West to the North-East of the Barents Sea is associated with strong environmental, compositional, functional traits and food-web structural variation. The North-East region of the Barents Sea, with the most distinct Arctic abiotic and biotic conditions, shows a peculiar food-web structure when compared with food-webs from the other investigated areas of the Barents Sea. These Arctic food-webs are characterized by lower connectance, higher modularity and lower degree of omnivory. The large difference in food-web configuration between the North-East Arctic region and the other regions of the Barents Sea is not simply explained by compositional or functional traits differences. The expansion of cod in the Arctic region shortens path lengths between trophospecies and results in a substantial food-web structural shift towards a more boreal connotation that strongly exceeds similar effects caused by the introduction of snow crab. The marked difference in impact on food-web structure by cod and snow crab can be explained by the greater degree of generalism and omnivory shown by cod. The strong structural change in Arctic food-webs imposed by climate-driven cod expansion goes in the direction of reduced robustness against environmental perturbations causing concerns for future cumulative risk to these ecosystems.

4.1 Spatial overlap and zoogeographic divide

The low spatial overlap between Barents Sea Arctic and boreal or Arcto-boreal trophospecies is reflected in the co-occurrences, which influence the probability of a feeding interaction being realized. Arctic trophospecies overlap and thereby can interact primarily with each other, with few exceptions of trophospecies with broader spatial distributions such as polar cod and Greenland shark, also co-occurring with boreal trophospecies. The biogeographic transition area coinciding with the Polar front thus determines the composition of species, their interactions, and the resulting food-web structure in Atlantic vs Arctic water masses. The environmental and compositional gradient analyses confirm the association between water masses and species composition. On the other hand, the modularity analysis of the metaweb weighted by spatial overlap does not identify modules for different biogeographic groups. The possible explanation is that the main structuring factors determining compartmentalization of trophic interactions in the metaweb are related to habitat affiliation, i.e., pelagic vs benthic compartments, and trophic level, i.e., predators vs consumers and basal trophospecies. In order to identify Arctic vs boreal modules in the weighted metaweb it would be therefore necessary to use a higher resolution in the modularity analysis.

The biogeographic separation of trophospecies in the Barents Sea metaweb implies that direct interactions are unlikely between trophospecies in Arctic vs Atlantic water masses, with the exceptions of some migratory species and broadly distributed ones. The spatial configuration of interactions influences the dynamics of the Barents Sea ecosystem and invites caution when representing it as fully connected. The spatial configuration of trophic interactions in the Barents Sea is such that many potential feeding links between Arctic and boreal species have not been realized historically but may occur under the ongoing climate driven redistributions of species (Kortsch et al., 2015; Pecuchet et al., 2020). The Bering Sea and other large marine ecosystems bordering the Arctic are also biogeographic transition zones (Mueter et al.,2021; Emblemsvåg et al., 2022a; Emblemsvåg et al., 2022b) where I expect to find similar patterns in spatial distribution of interactions that might affect spatial variation in food-web structure.

4.2 Spatial variation in food-web configuration

The Barents Sea food-webs display ample spatial variation in configuration, with the main gradient of variation being associated with ocean climate and differences between Arctic vs Atlantic water masses. This main structural gradient is associated with the food-web properties of modularity, higher in the Arctic region, and connectance and omnivory, higher in the Atlantic region. The above food-web properties principally responsible for spatial variation in food-web structure are affected by functional traits, such as degree of dietary generalism, which show zoogeographic differences (Kortsch et al., 2019; Pecuchet et al., 2020; Frainer et al., 2021; Pecuchet et al., 2022). An interesting finding is the sharp structural separation along the main gradient of food-web variation of three Arctic NoBa polygons from the other investigated areas. The three Arctic polygons are situated furthest North-East in the

Barents Sea, close to the Kara Sea, with which they exchange species. Differences in food-web structure between these three Arctic food-webs and the other investigated food-webs are much larger than expected based on compositional or traits differences alone.

The ocean climate gradient is aligned with the main compositional and food-web structural gradient concerning biogeographic variation (Kortsch et al., 2019). Along this gradient, environmental conditions and filtering translate into characteristic sets of species' adaptations and traits that influence feeding links and food-web structure (Frainer et al. 2017, Kortsch et al. 2019, Pecuchet et al. 2022). Fish play an important role in the organization of aquatic food webs and their traits differ substantially between Arctic and boreal species (Frainer et al. 2017 Frainer et al., 2021). Body size is known to affect predator-prey interactions in marine ecosystems (Belgrano et al., 2005), with bigger body size in fish relating to higher degree of omnivory and higher trophic level (Keppeler et al., 2020). In the Arctic Barents Sea, fish sizes are smaller than in the warmer South-West Atlantic waters, making for distinct diets and feeding behaviour, with important consequences for food-web structure (Frainer et al., 2017). The smaller Arctic fish are primarily benthivores with narrow diets, feeding on prey at low trophic levels (Frainer et al. 2017), resulting in few links and low connectance, sharp distinction between benthic and pelagic compartments and high modularity, and a low degree of omnivory (Ingvaldsen et al. 2021). Boreal, demersal fish species are characterized by being large, generalist species which include pelagic prey in their diets (Frainer et al., 2017; Townhill et al., 2021). These characteristics result into more highly connected food-webs that are less modular and have a higher degree of omnivory (Kortsch et al. 2015; Pecuchet et al. 2022).

The clear separation in food-web metrics between the three Arctic NoBa polygons in the North-East and the other polygons contrasts with the expectation of a gradual food-web structural change accompanying gradual compositional change. The results show a more complex relationship between composition and food-web structure, with small to intermediate compositional differences leading to large food-web structural differences, and the emergence of a distinct Arctic cluster. Traits composition is also insufficient to explain the large food-web structural differences, suggesting that certain combinations of trophospecies give rise to distinct food-web structural features in the Arctic. An implication of the finding is that few species substitutions or additions, e.g., driven by distributional shifts or invasion, could be sufficient to substantially alter food-web structure in the Arctic (Kortsch et al., 2015; Pecuchet et al., 2020).

The zoogeographic divide between boreal and Arctic species has been reported in other high latitude ecosystems (Allen & Smith, 1988; Mecklenburg et al., 2011; Sigler et al., 2017). Although information on the resulting spatial variation in marine food-webs is still lacking (Kędra et al., 2015), studies on biological traits have emerged in the last years (Rand et al., 2018; Degen & Faulwetter, 2019, Emblemsvåg et al 2022a). Arctic species show characteristic configurations of traits that differ from boreal ones and influence feeding behaviour and links (Emblemsvåg et al., 2022a). Thus, biogeographic differences in food web structure are expected on a pan-Arctic scale. Warming is leading to a borealization of Arctic communities bringing new traits and feeding links that reorganize food web structure in the Arctic (Mueter et al., 2021; Emblemsvåg et al., 2022a; Emblemsvåg et al., 2022b).

4.3 Reconfiguration of food-web structure by incoming species

The climate driven expansion of cod into Arctic regions of the Barents Sea triggers a substantial reorganization of the food-webs as indicated by the widespread shortening of path lengths connecting trophospecies. The generalist, omnivore cod establishes many new links in Arctic food-webs (Johannesen et al., 2020; Pecuchet et al., 2020), which increase the connectance, and couple food-web compartments reducing modularity (Kortsch et al 2015; Pecuchet et al. 2020). Also, the mean degree of omnivory, which is low among Arctic species, is markedly increased by cod. The effect of invasion by the generalist snow crab has a similar character to that of cod, with a borealization of Arctic food-web properties, but with much smaller magnitude. The snow crab has fewer Arctic prey species than cod and its feeding links are restricted primarily to the benthic compartment of the food-web (Zakharov et al., 2021). Therefore, its effect on modularity and connectance is less pronounced. The combined effect of Arctic colonization by cod and snow crab is additive, increasing the magnitude but not the direction of change.

Incoming boreal, generalist species such as cod increase the number of feeding links within Arctic food-webs and the coupling of the benthic and pelagic compartments (Kortsch et al., 2015). With warming, cod expands its distribution poleward establishing new feeding links with Arctic species (Pecuchet et al., 2020). As a generalist, cod benefits from the high food availability it finds in the Arctic regions, where large fish predators are not common (Johannesen et al., 2020). Its feeding on different functional groups, across benthic and pelagic compartments, contrasts with the characteristic feeding links associated with small Arctic benthivore fish (Frainer et al., 2017), reducing modularity of recipient Arctic food-webs. Cod is but one of several boreal, large generalists that are moving or are expected to move further north in the Barents Sea (Pecuchet et al., 2020). It is expected that these generalists will have similar effects on the Arctic food-web, possibly magnifying the overall impact (Bartley et al., 2019; Pecuchet et al., 2020). The borealization of the Arctic is not limited to the Barents Sea. Generalist boreal fish and other species are entering the warming Arctic, triggering structural changes of Arctic communities (Mueter et al., 2021; Emblemsvåg et al., 2022a; Emblemsvåg et al., 2022b; von Biela et al., 2023). Despite the lack of highly resolved studies on Arctic marine food-webs outside of the Barents Sea, the effects of borealization can be expected to be similar across the Arctic.

Snow crab has successfully established in the North-East Barents Sea since it was first reported in the 1990s (Alvsvåg et al., 2009; Agnalt et al., 2011; Mullowney et al., 2018). Similar to cod, snow crab is a generalist species, but it mostly feeds on the benthic compartment (Zakharov et al., 2021). The introduction of snow crab has a similar but lesser effect on the Arctic food-webs structure than cod since its influence is limited to the benthic compartment. Cod is one of the few predators of snow crab in the Barents Sea (Holt et al., 2019; Holt et al., 2021), potentially exerting a top-down control on the snow crab population when they co-occur. Yet, the outcome of the interaction of these species in the Barents Sea is still unclear. Cod and snow crab have different affinities for abiotic conditions, which might affect their future spatial overlap. Snow crab is a cold-water species with juveniles preferring Arctic waters, which is expected to influence the spatial character of its expansion in the Barents Sea. Arctic species have a slower turnover rate and productivity than temperate species, cod could thereby deplete its prey availability, which could slow down its poleward expansion (Johannessen et al 2020). During the last few years, and beginning in 2018, the Arctic Barents Sea experienced a cooling episode that granted snow crab the conditions to expand further south while stalling cod's expansion. Both species are highly valuable for fisheries and could be managed so as to limit their impact on the Arctic Barents Sea biodiversity, but their interactions complicate the identification of effective management solutions.

The borealization of Arctic food-webs leads to food-web reorganization that has implications for ecosystem vulnerability to environmental perturbations. Shorter path lengths imply greater risk of food-web mediated indirect transmission of perturbation effects. Reduced modularity and increased connectance promote a greater spread of perturbation effects across the food-web, so that many more species may be impacted (Teng & McCann, 2004; Kortsch et al., 2015). Borealization thereby reduces internal food-web stability and increases systemic risk. The increased vulnerability of Arctic food-webs is concerning given that climate change will likely increase the nature, frequency, and strength of environmental perturbations due to projected higher climate variability and expanding human activities.

5 CONCLUSIONS

Arctic food-webs are experiencing rapid compositional change and rewiring due to climate driven redistributions and invasions. Several incoming species are generalists that increase connectance and reduce modularity of recipient food-webs, increasing ecosystem vulnerability to multiple stressors. This thesis shows that a few generalist species like cod are sufficient to strongly modify Arctic food-webs structure in the direction of higher vulnerability. Such a finding highlights the importance of including food-web reconfiguration by incoming species into risk assessment and management plans of marine ecosystems.

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Appendix

Table S1. Environmental data of the NoBa polygons: mean water temperature (ºC), mean salinity (PSU), mean depth (m), and mean number of days per year with sea-ice cover.

	T (ºC)	DEPTH (M)	S(PSU)	SEAICE (DAYS/YEAR)
5	7.547	210.100	34.935	0.800
21	4.742	326.912	34.941	58.142
22	3.011	268.065	34.671	61.446
23	4.450	275.568	34.974	46.466
24	2.464	73.500	34.707	67.028
25	6.151	404.071	35.094	0.012
26	2.049	186.086	34.810	107.241
27	7.045	338.333	35.008	1.200
30	6.460	315.000	34.878	0.306
33	4.668	192.735	34.801	0.647

34	4.368	99.125	34.473	6.075
35	3.786	74.250	33.878	42.950
37	1.960	86.083	34.035	90.250
38	3.128	142.687	34.755	30.060
39	3.047	308.636	34.983	0.424
40	3.970	252.218	35.031	3.727
41	5.894	293.137	35.009	0.032
42	3.564	309.765	35.034	28.490
43	2.320	217.548	35.020	22.742
44	0.961	276.117	34.813	129.585
45	1.196	176.021	34.800	59.438
46	-0.012	328.250	34.634	210.750
47	1.130	210.177	34.775	154.031
48	0.778	299.184	34.550	231.804

49	1.376	260.335	34.539	222.626

Table S2. Weighted community mean traits.

	CONTINUOUS (CM)	SUSPENSION FEEDER	DEPOSIT FEEDER	PREDATOR	BENTHIC	BENTHO/ PELAGIC	PELAGIC	TROPHIC LEVEL	OMNIVORY INDEX	IN DEGREE	OUT DEGREE
5	68.97	0.56	0.54	1.83	1.53	0.76	0.94	3.08	0.22	11.17	10.49
21	90.22	0.68	0.53	1.83	1.50	0.75	0.96	3.07	0.21	10.01	10.70
22	97.55	0.71	0.54	1.76	1.60	0.68	0.91	3.03	0.21	10.21	10.58
23	81.38	0.65	0.48	1.86	1.52	0.73	0.94	3.05	0.19	9.90	10.25
24	95.96	0.67	0.50	1.75	1.64	0.67	0.88	3.01	0.20	10.23	9.53
25	84.40	0.64	0.53	1.79	1.51	0.73	0.99	3.00	0.20	9.57	10.64
26	72.79	0.63	0.51	1.83	1.60	0.71	0.92	3.02	0.21	10.14	10.80
27	75.58	0.61	0.54	1.80	1.52	0.73	0.96	3.05	0.20	10.03	10.88
30	84.17	0.67	0.56	1.75	1.54	0.74	0.94	3.01	0.21	9.62	10.50
33	79.86	0.61	0.54	1.83	1.50	0.78	0.94	3.10	0.22	10.60	10.86
34	85.04	0.58	0.55	1.82	1.55	0.76	0.90	3.09	0.19	10.24	10.39
35	92.14	0.56	0.57	1.81	1.62	0.70	0.88	3.11	0.20	10.32	9.97

37	85.04	0.60	0.58	1.82	1.69	0.70	0.81	3.07	0.20	9.43	9.93
38	90.81	0.62	0.59	1.80	1.72	0.68	0.80	3.08	0.20	10.14	10.22
39	98.89	0.73	0.53	1.76	1.56	0.71	0.95	3.04	0.19	9.33	11.27
40	88.50	0.63	0.61	1.76	1.64	0.68	0.88	3.03	0.22	9.65	11.03
41	84.49	0.63	0.58	1.77	1.55	0.76	0.91	3.02	0.21	9.83	10.76
42	70.07	0.63	0.50	1.83	1.54	0.73	0.95	3.04	0.21	9.48	11.27
43	83.77	0.62	0.53	1.86	1.62	0.69	0.89	3.07	0.22	9.70	10.82
44	83.30	0.72	0.48	1.85	1.55	0.69	0.99	3.04	0.20	9.57	11.64
45	106.53	0.72	0.49	1.84	1.58	0.68	0.95	3.07	0.20	9.42	10.79
46	77.75	0.62	0.50	1.91	1.52	0.75	0.96	3.10	0.22	10.17	11.90
47	73.91	0.66	0.51	1.87	1.50	0.73	0.97	3.06	0.22	10.69	11.04
48	71.58	0.66	0.47	1.90	1.52	0.75	0.92	3.08	0.21	10.63	10.90
49	81.98	0.67	0.53	1.84	1.57	0.72	0.90	3.07	0.21	10.29	10.91

Table S3. Calculated food-web metrics for the 25 polygons of the Barents Sea's original composition, and the food-web metrics of polygons 44, 45 and 46 after introducing cod (44COD, 45COD, 46COD), snow crab (44SC, 45SC, 46SC), and both species (44CODSC, 45CODSC, 46CODSC).

	S	**L**	**LD**	**C**	**CLUST**	**COMP**	**OMNI**	**PRED PREY**	**CAN**	**BAS**	**TOP**	**INT**	**GEN SD**	**VUL SD**	**MEAN SWTL**	**MEAN PATH**
5	132	860	6.52	0.05	0.26	0.28	0.21	0.88	0.11	0.17	0.05	0.78	1.30	1.26	2.98	2.14
21	178	1354	7.61	0.04	0.23	0.28	0.20	0.96	0.12	0.07	0.03	0.89	1.42	1.27	2.96	2.23
22	168	1342	7.99	0.05	0.26	0.28	0.22	0.94	0.11	0.10	0.04	0.86	1.37	1.28	3.01	2.75
23	162	1224	7.56	0.05	0.25	0.28	0.21	0.91	0.12	0.12	0.04	0.84	1.38	1.33	2.96	2.20
24	142	969	6.82	0.05	0.23	0.31	0.19	0.91	0.11	0.13	0.05	0.82	1.33	1.24	2.83	2.50
25	138	953	6.91	0.05	0.26	0.28	0.22	0.88	0.14	0.16	0.04	0.80	1.35	1.27	2.89	2.22
26	165	1288	7.81	0.05	0.24	0.28	0.23	0.96	0.11	0.08	0.04	0.87	1.37	1.30	2.93	2.70
27	136	960	7.06	0.05	0.27	0.27	0.21	0.92	0.13	0.13	0.05	0.82	1.35	1.22	2.93	2.26
30	150	1099	7.33	0.05	0.25	0.29	0.22	0.93	0.12	0.11	0.04	0.85	1.43	1.24	2.90	2.24
33	148	1152	7.78	0.05	0.27	0.27	0.20	0.93	0.14	0.11	0.04	0.85	1.39	1.21	2.87	2.17
34	134	928	6.93	0.05	0.24	0.29	0.18	0.92	0.13	0.12	0.04	0.84	1.38	1.15	2.83	2.09
35	114	740	6.49	0.06	0.24	0.28	0.19	0.98	0.11	0.08	0.06	0.86	1.40	1.07	2.72	2.02

37	119	682	5.73	0.05	0.21	0.30	0.19	0.96	0.09	0.09	0.05	0.86	1.42	1.18	2.71	2.02
38	143	1016	7.10	0.05	0.23	0.27	0.18	0.96	0.12	0.08	0.04	0.88	1.41	1.24	2.78	2.06
39	150	1052	7.01	0.05	0.25	0.29	0.19	0.90	0.13	0.13	0.04	0.83	1.29	1.33	2.84	2.15
40	142	943	6.64	0.05	0.25	0.29	0.19	0.89	0.12	0.14	0.04	0.82	1.38	1.33	2.85	2.16
41	141	952	6.75	0.05	0.26	0.28	0.21	0.89	0.13	0.14	0.04	0.82	1.37	1.29	2.90	2.24
42	147	1060	7.21	0.05	0.25	0.29	0.21	0.92	0.12	0.11	0.03	0.86	1.38	1.30	2.88	2.08
43	155	1084	6.99	0.05	0.23	0.30	0.20	0.93	0.11	0.11	0.04	0.85	1.41	1.36	2.83	2.12
44	141	663	4.70	0.03	0.16	0.36	0.18	0.84	0.07	0.20	0.05	0.75	1.08	1.63	2.76	2.11
45	146	684	4.68	0.03	0.15	0.35	0.16	0.86	0.07	0.18	0.05	0.77	1.13	1.59	2.72	2.09
46	137	665	4.85	0.04	0.16	0.34	0.17	0.86	0.08	0.19	0.06	0.75	1.10	1.59	2.71	2.02
47	153	1023	6.69	0.04	0.24	0.30	0.20	0.94	0.10	0.10	0.05	0.84	1.31	1.35	2.86	2.17
48	162	1107	6.83	0.04	0.24	0.28	0.19	0.91	0.10	0.14	0.05	0.81	1.31	1.41	2.87	2.10
49	169	1309	7.75	0.05	0.24	0.28	0.19	0.98	0.11	0.07	0.04	0.89	1.42	1.28	2.94	2.11
44COD	141	706	5.01	0.04	0.19	0.34	0.18	0.86	0.07	0.18	0.05	0.77	1.31	1.55	2.77	2.06

45COD	146	726	4.97	0.03	0.17	0.33	0.16	0.88	0.07	0.16	0.05	0.79	1.36	1.51	2.73	2.05
46COD	137	706	5.15	0.04	0.19	0.32	0.17	0.88	0.08	0.17	0.06	0.77	1.34	1.50	2.71	2.01
44SC	141	663	4.70	0.03	0.16	0.36	0.18	0.84	0.07	0.20	0.05	0.75	1.08	1.63	2.76	2.11
45SC	146	684	4.68	0.03	0.15	0.35	0.16	0.86	0.07	0.18	0.05	0.77	1.13	1.59	2.72	2.09
46SC	137	665	4.85	0.04	0.16	0.34	0.17	0.86	0.08	0.19	0.06	0.75	1.10	1.59	2.71	2.02
44CODSC	142	734	5.17	0.04	0.19	0.33	0.18	0.89	0.08	0.15	0.05	0.80	1.32	1.51	2.77	2.08
45CODSC	147	756	5.14	0.03	0.17	0.32	0.16	0.91	0.07	0.14	0.05	0.82	1.37	1.47	2.73	2.07
46CODSC	138	734	5.32	0.04	0.19	0.32	0.18	0.92	0.09	0.14	0.06	0.80	1.35	1.47	2.72	2.02

Table S4. List of the food-web metrics used in this study, their definitions, and implications in an ecological context. (Modified from Kortsch et al., 2019).

METRIC	DEFINITION	STRUCTURAL AND DYNAMICAL IMPLICATIONS
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.
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
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.
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 is distributed.

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. Like connectance, clustering may influence the stability of the food-web
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.
DEGREE OF OMNIVORY	Degree 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 degrees of omnivory may stabilize communities and may diffuse top-down influences through the food-webs and thereby reduce the probability of trophic cascades.

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.
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.
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.
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.
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.
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 degree of omnivory.

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.
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.
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.

Table S5. Summary table of principal component analysis results for the environmental data.

	COMP. 1	**COMP. 2**	**COMP. 3**	**COMP. 4**
STANDARD DEVIATION	1.457	1.114	0.603	0.334
PROPORTION OF VARIANCE	0.553	0.323	0.095	0.029
CUMULATIVE PROPORTION	0.553	0.876	0.971	1.000

Table S6. Summary table of principal component analysis results for the Barents Sea food-web metrics with the original composition.

	COMP. 1	**COMP. 2**	**COMP. 3**	**COMP. 4**
STANDARD DEVIATION	3.119	1.600	1.116	0.940
PROPORTION OF VARIANCE	0.633	0.166	0.081	0.058
CUMULATIVE PROPORTION	0.633	0.800	0.881	0.939

Table S7. Frequencies of shortest path lengths for the Arctic NoBa polygons (44, 45, 46) without and with cod (COD) and/or snow crab (SC).

		0	**1**	**2**	**3**	**4**	**5**
NO COD OR SC	*44*	0.00714	0.06398	0.46418	0.41143	0.05306	0.00020
	45	0.00690	0.06145	0.46154	0.41455	0.05527	0.00028
	46	0.00735	0.06791	0.48086	0.40192	0.04163	0.00032
COD	*44*	0.00709	0.06982	0.52663	0.36115	0.03531	0.00000
	45	0.00685	0.06709	0.53209	0.35832	0.03565	0.00000
	46	0.00730	0.07384	0.54270	0.35015	0.02600	0.00000
SC	*44*	0.00709	0.06569	0.47452	0.40612	0.04638	0.00020
	45	0.00685	0.06324	0.47251	0.41011	0.04701	0.00028
	46	0.00730	0.06969	0.49145	0.39427	0.03698	0.00032
COD & SC	*44*	0.00704	0.07151	0.53610	0.35499	0.03035	0.00000
	45	0.00680	0.06886	0.54209	0.35235	0.02989	0.00000
	46	0.00724	0.07561	0.55230	0.34205	0.02279	0.00000