


Spatio-temporal turnover and drivers of benthic-demersal community and food web structure in a high-latitude marine ecosystem

Laurene Pecuchet¹  | Lis Lindal Jørgensen² | Andrey V. Dolgov^{3,4,5} | Elena Eriksen⁶ | Berengere Husson⁶ | Mette Skern-Mauritzen⁶ | Raul Primicerio¹

¹UiT – The Arctic University of Norway, Tromsø, Norway

²Institute of Marine Research, Tromsø, Norway

³Polar Branch of Russian Federal Research Institute of Fisheries and Oceanography (PINRO named after N.M.Knipovich), Murmansk, Russia

⁴Murmansk State Technical University, Murmansk, Russia

⁵Tomsk State University, Tomsk, Russia

⁶Institute of Marine Research, Bergen, Norway

Correspondence

Laurene Pecuchet, UiT – The Arctic University of Norway, Tromsø, Norway.
Email: laurene.pecuchet@uit.no

Funding information

arktis 2030, Grant/Award Number: QZA-15/0137; Norges Forskningsråd, Grant/Award Number: 288192

Editor: Sophie von der Heyden

Abstract

Aim: Assess the spatial and temporal turnover of benthic-demersal marine fauna by integrating ecological metrics at the community and food web levels and evaluate their main environmental and anthropogenic drivers.

Location: Barents Sea.

Method: We analysed data of benthic and benthic-pelagic fish and megabenthic invertebrates caught in the Barents Sea ecosystem survey in August–September 2009–2017 to characterize the spatial and temporal variability of benthic-demersal communities and food webs. We used a trait dataset and highly resolved benthic-demersal food web to calculate community and food web metrics in space and time. We spatially clustered the community and food web based on their properties using archetypal analysis and investigated their co-variation with environmental and fishing pressure using (hierarchical) redundancy analysis.

Result: The community and food web metrics partitioned the Barents Sea into four sub-regions where different pressures act on the benthic-demersal fauna, such as sea ice loss and fisheries. Multiple community metrics (e.g. mean body length and trophic level) varied along an environmental gradient of annual mean sea bottom temperature, trawling intensity and ice-cover, whereas multiple food web metrics (e.g. nestedness and connectance) varied along an environmental gradient of depth and sediment composition. Communities had higher biomass-weighted variability in body size and omnivory values in areas where the Atlantic and Arctic water masses mix. Several food web and community metrics co-varied (e.g. food chain length and mean trophic level). We found no clear temporal trends in the ecological metrics in any of the four sub-regions, but the metrics had large inter-annual variability with some local minima or maxima coinciding with high sea temperature and ice-cover anomalies.

Conclusion: Analyses at the community and food web level are seldom integrated in ecological studies, while this integration gives complementary information to assess patterns and drivers of ecosystem state and to better prioritize conservation efforts.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Diversity and Distributions* published by John Wiley & Sons Ltd.

KEYWORDS

arcto-boreal ecosystem, Barents Sea, fish-benthos communities, fishing pressure, functional diversity patterns, marine food web, spatial turnover

1 | INTRODUCTION

Species distributions are constrained by environmental conditions and biotic interactions, shaping biogeographic patterns at the macro-ecological scale (Chase & Leibold, 2003; Soberón, 2007). In the case of strong environmental control on species distribution, species that co-exist within an ecological assemblage are likely to share similar ecological traits that enable them to survive under local environmental conditions (Keddy, 1992; Violle et al., 2007). This has notably been shown in the marine realm, where the trait composition of fish communities is spatially structured along environmental gradients, such as salinity and depth gradient (Beukhof et al., 2019; Mindel, Neat, et al., 2016; Mouillot et al., 2007; Pecuchet et al., 2016). The spatial and temporal variation, that is, turnover, in community taxonomic and trait composition is well studied across realms and taxa (e.g. Blowes et al., 2019; Magurran et al., 2015; Pecuchet et al., 2018; Soininen et al., 2018), and several studies have also investigated the topological turnover in food web properties resulting from changes in taxonomic composition (Albouy et al., 2019; Kortsch et al., 2021, 2019; Olivier et al., 2019) and/or feeding preferences (e.g. rewiring [Olesen et al., 2011]). Whereas spatial turnover patterns of community and food web have been analysed separately, their joint study is largely unexplored. Yet, such a joint study could inform how community structure and functions influence food web properties across multiple-stressor gradients (Frelat et al., 2022; Tylianakis & Morris, 2017).

A food web represents the feeding interactions between organisms co-occurring in a specific location, and are as such arising from species distribution, and local community composition. With their myriad of interactions, food webs are inherently complex. This complexity can be summarized into analytical metrics, that is, food web properties, which are emerging from the configurations and strengths of feeding interactions between species (Delmas et al., 2019). Feeding interactions are largely mediated by the traits of a predator (consumer) and its prey (resource) (Brose et al., 2019). The trait composition of a community is thus likely to influence the properties of the trophic network emerging from the feeding interactions within this community. As the trait composition of a community is varying along environmental gradients, it is thus expected that food web structure will also co-vary along these gradients (Pellissier et al., 2018). For example, in the marine environment, feeding interactions are highly structured by the predator and prey body size (Brose et al., 2019; Laigle et al., 2018; Pecuchet et al., 2020), and the body size structure within ecological communities can vary along environmental gradients (e.g. fish size along depth gradients [Mindel, Webb, et al., 2016]). Analysing co-variation between community trait composition and the properties of ecological networks is thus a key step towards understanding the impact of functional trait diversity on food web properties and functions (Gravel et al., 2016).

The Barents Sea is a highly productive arcto-boreal ecosystem that sustains ecologically and commercially important fish and invertebrate populations (Haug et al., 2017). The Barents Sea benthodemersal fish and invertebrate communities are spatially structured and characterized by a biogeographic divide between boreal species, which are distributed in the southwest Atlantic-dominated waters, and Arctic species, which are distributed in the north and northeast Arctic-dominated waters (Fossheim et al., 2015; Johannesen et al., 2017; Jørgensen et al., 2015). Food web properties in the Barents Sea are also structured along environmental gradients of sea temperature and ice-cover (Kortsch et al., 2019). The Barents Sea ecosystem has been strongly affected by fishing activities and more recently by other human activities such as oil and gas production and shipping (ICES, 2019). The ecosystem is changing fast, warming at a rate exceeding the global average, and with a diminishing sea ice extent (Smedsrud et al., 2013), and an associated decrease in salinity and stratification (Lind et al., 2018). These environmental alterations have led to a restructuring in species biomass and distribution, with a northward shift of both boreal and Arctic communities and increased biomass of boreal species in the historically Arctic part of the Barents Sea (Fossheim et al., 2015; Ingvaldsen et al., 2021). This rapid borealization may have profound consequences on the functioning and vulnerability of the Barents Sea ecosystem, as the boreal species share different traits and life-history strategies than their Arctic counterparts. For example, Arctic fish communities are characterized by the dominance of small benthivorous species while the boreal, northward-expanding, species are characterized by large body size and piscivorous diet (Frainer et al., 2017). Due to their generalist diet, these species might affect the structure and vulnerability of the Arctic food web by increasing the connectivity between the benthic and pelagic compartments (Kortsch et al., 2015; Pecuchet et al., 2020). Community and food web spatial patterns in marine ecosystems, including the Barents Sea, have not yet been studied in an integrative way, but are studied in isolation using different spatial scales and focusing on different compartments and taxonomic resolutions. Yet, an integrative comparison of spatial patterns in community- and food web-level properties is needed to assess their co-variation and to promote an understanding of how food web structure might emerge from the composition at the community level. In addition, it is still unclear whether it is the same set of environmental and anthropogenic pressures that structure community- and food web-level properties.

In this study, we combine the information of a trait dataset and an extensive food web with bottom-trawl catch data from an ecosystem survey to calculate biomass-weighted community metrics and unweighted food web properties. We assess spatial and temporal changes in the community and food web properties of the benthodemersal compartment of the Barents Sea (fish and

macrobenthic-invertebrates) and relate them to variations in environmental and fishing pressures. Specifically, we ask: (1) what are the spatial patterns and co-variation of the benthic-demersal community and food web properties, (2) are these patterns related to spatial patterns in the environment and trawling intensity, (3) have the community and food web properties changed in the Barents Sea during the last decade (2009–2017). Based on prior knowledge of the Barents Sea ecosystem and its recent dynamics (e.g. Eriksen et al., 2021; Fosshem et al., 2015; Frainer et al., 2017; Johannesen et al., 2017; Jørgensen et al., 2015; Kortsch et al., 2019), we expect that the communities and food web metrics are spatially structured along known environmental gradients in the Barents Sea, especially along the south–north gradient in temperature and sea ice-cover (Figure 1). Spatial patterns of fishing are influenced by diverse social, economic, environmental and ecological factors (van Putten et al., 2012); here, we expect that trawling activities, which target specific benthic-demersal communities composed of commercial fish and invertebrate species, will, in turn, varies along this south–north ecological and sea ice-cover (i.e. accessibility) gradients. Temporally, we expect to see the most changes in the communities and food webs in the Arctic part of the Barents Sea, that is, we expect different temporal trends between boreal and Arctic ecosystems and that these changes are mainly due to changes in species biomass rather than species occurrence (i.e. larger changes in biomass-weighted metrics than unweighted food web metrics).

2 | MATERIAL AND METHODS

2.1 | Benthic-demersal communities

Data on the presence and biomass of bottom-dwelling fish and megabenthos, that is, large benthic invertebrates, in the Barents Sea were obtained from the joint Barents Sea Ecosystem Survey

annually conducted by Institute of Marine Research (IMR, Norway) and Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia, since 2019—Polar branch of Russian Federal Research Institute of Fisheries and Oceanography (VNIRO) (Eriksen et al., 2018). Sampling was performed in August–September for the period 2009–2017. Each year demersal fish and megabenthos were sampled at spatially predetermined stations (~270) positioned along a regular grid (~65 km between stations) using Campelen 1800 bottom trawl at a mean towing speed of 3 knots during 15 mn equivalent to a towing distance of ~1.4 km. The mean vertical trawl opening is 25 m and the mesh size is 80 mm (stretched) in the front and 22 mm at the codend, allowing the capture and retention of small fish and megabenthos from the seabed. The catchability of each megabenthos species by the scientific bottom trawl will vary depending on the species length and body shape; we expect body sizes larger than the mesh size (22 mm) to be better retrieved inside the trawl. We, therefore, consider the sampling of megabenthos species to be semi-quantitative. This semi-quantitative approach allows us to compare values in space and time, and it has proven valuable in long-term monitoring (Degen et al., 2016; Jørgensen et al., 2022, 2019). All individuals of fish and invertebrates caught in the trawl hauls were sorted and identified to the lowest taxonomic level possible, their wet biomass is weighted, and abundance was counted and standardized by unit swept area. Not all individuals were identified at the species level, but for simplicity, we will hereafter refer to these different entities, both species and higher taxonomic grouping, as taxa.

We divided the Barents Sea on an equal-area grid composed of 60 hexagonal cells of about 23,300 km² and the cell centres about 165 km apart. The grid was computed using the *dggridR* package (Barnes et al., 2018). To characterize the spatial patterns in benthic-demersal community composition, we did, for each grid cell and all years combined, sample-based effort standardization by assembling benthic-demersal communities from a random draw of

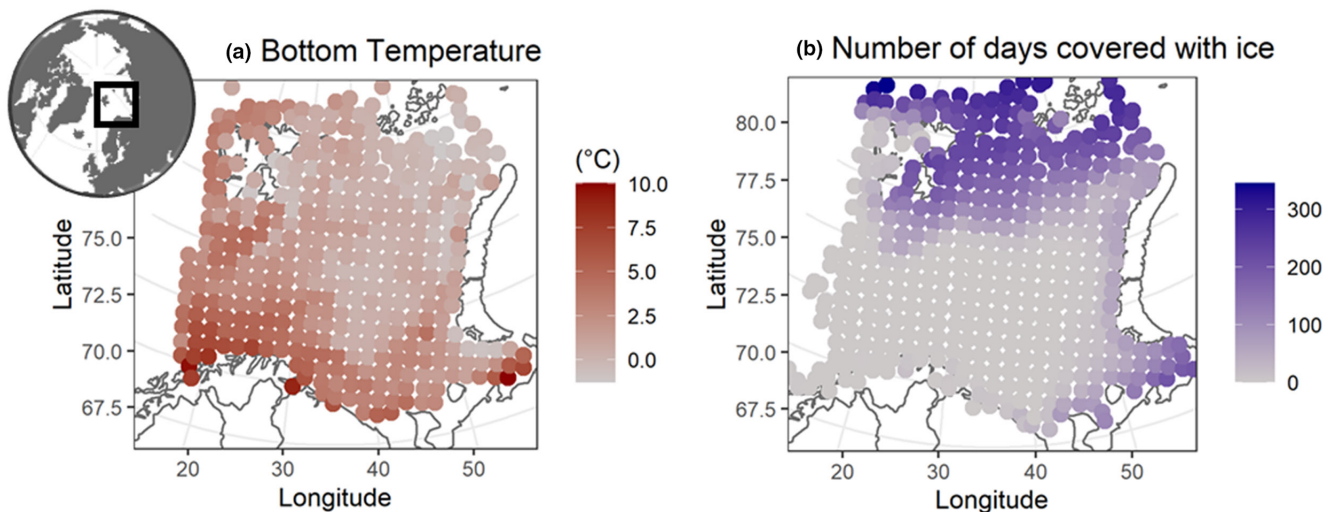


FIGURE 1 Location of the Barents Sea and (a) bottom temperature at the time of the Barents Sea ecosystem survey (August–September) and (b) number of days within a year with sea ice-cover averaged for the study period 2009–2017

10 megabenthos and demersal fish sampling stations. This effort standardization permits the elimination of possible bias due to differences in sampling effort between grid cells. We reiterated this random draw 100 times, and for each iteration taxa biomass and abundance were calculated as the sum of their biomass and abundance density (kg or number/haul) across the 10 randomly selected stations. This resulted in 100 benthic-demersal communities assembled for each grid cell using the same sampling effort (10 stations). Finally, all benthic-demersal communities were filtered to only retain the taxa that are documented in the meta food web (metaweb, Planque et al., 2014, see below).

2.2 | Food web

The benthic-demersal food web was derived from an extensive meta food web (metaweb) documenting 2461 feeding links between 239 taxa that inhabit the Barents Sea (Planque et al., 2014), ranging from plankton to benthic invertebrates, fish, sea birds and marine mammals. A taxon can refer to various levels of taxonomic resolution, from species (e.g. *Gadus morhua*) to class (e.g. *Hydrozoa*), with this set of one or more species sharing the same resources and predators (Yodzis & Winemiller, 1999). The feeding links were documented from peer-reviewed literature, reports, personal communication with experts or inferred from taxonomically similar species and spanned the period from 1927 to 2012 (Planque et al., 2014). In addition, we used information on fish diet from the 2015 Norwegian-Russian "Year of the stomach" (Eriksen et al., 2021) to update and improve the benthic-demersal food web. Here, we are only studying the taxa that were recorded in the ecosystem survey bottom trawls; we thus did a subset of the metaweb to keep only the fish and the invertebrates sampled in the trawls (see species list in Table S1). For appropriate trophic level estimation, we retained the basal groups' *phytoplankton* and *detritus*, and the group *zooplankton* in the food web, and considered them present across the entire Barents Sea (i.e. present in all grid cells). The final benthic-demersal food web used in this study had 111 taxa and 1082 feeding links (Figure S1). On average per grid cell, 99.3% (94.9%–100%) of megabenthos and 99.5% (98.7%–100%) of demersal fish individuals sampled were included in the food web (Figure S2), albeit sometimes specified at a higher taxonomic level within the food web.

2.3 | Community and food web metrics

To investigate spatial patterns in community and food web composition, we calculated for each grid cell 18 community and food web metrics based on the assembled 100 benthic-demersal communities. These metrics can be calculated based on changes in taxonomic composition (presence/absence), taxa biomass, prey biomass in stomach contents (feeding preferences) or energy fluxes (Dunne et al., 2004; Gauzens et al., 2019; Kortsch et al., 2021). Each metric type can reveal different facets of community and food web

spatial and temporal changes, and it is thus important to use multi-type metrics to obtain a more comprehensive assessment (Kortsch et al., 2021; Olivier et al., 2019). The calculated food web properties were the number of taxa, number of feeding links, feeding link density, connectance, modularity, nestedness and average food chain length (Table 1). These metrics were based on taxa presence-only (unweighted). Modularity and food chain length were calculated using the R package *igraph* (Csardi & Nepusz, 2006) and nestedness the R package *vegan* (Oksanen, 2017). To complement the food web properties, we calculated metrics to characterize the composition of the benthic-demersal communities: the total biomass, the biomass evenness, the biomass ratio between fish and megabenthos, the biomass-weighted mean and variability of trophic level, omnivory, generality and body size. Trophic level represents the feeding position of a taxon in the food web, here it goes from 1 (primary producers) to 4.2 (Greenland shark *Somniosus microcephalus*). Generality represents a taxon's number of documented preys in the metaweb, here, going from one (e.g. strict detritivorous) to 85 for Atlantic cod *Gadus morhua*. Omnivory indicates the extent to which a taxon feed on multiple trophic levels, here it goes from zero (e.g. strict detritivorous) to 0.83 for starfishes *Ophiura* sp. Body size, obtained from (Pecuchet et al., 2020), represents the size in centimetres of a taxon's longest body axis and was log-transformed due to right-skewed distribution. The values of trophic level, omnivory and generality were calculated for each taxon using the Barents Sea benthic-demersal metaweb and were thus kept constant through space and years (i.e. each taxon is assigned one value based on the metaweb). The trophic level and omnivory were calculated using the R package *NetIndices* (Kones et al., 2009). The food web- and community-level metrics were calculated using the same input data, that is, by using the 100 benthic-demersal communities assembled per grid cell that were filtered to only retain the taxa present in the metaweb. Biomass was log-transformed before calculating the biomass-weighted mean and variability indices due to right-skewed biomass distribution, and by doing so to avoid the indices only depicting spatial turnover of dominant and widely distributed fish species (such as Atlantic cod and haddock *Melanogrammus aeglefinus*). In addition, the bottom trawl gear has a higher catchability for fish than megabenthos due to the height-width of the trawl allowing not only fish from the seabed, but also semi-pelagic to enter the trawl, log-transforming the biomass permits to increase the importance of megabenthos species in the calculations of the biomass-weighted metrics. The ratio of fish-to-megabenthos biomass was calculated using absolute fish and megabenthos biomass, and the obtained ratio was then log-transformed to approximate symmetrical data distribution. Spatial maps of the ecological metrics can be found in (Figures S3–S5).

2.4 | Barents Sea environment

We selected 18 variables to characterize the Barents Sea environmental conditions and demersal fishing pressure. These variables were further split into three variable types that characterize the

TABLE 1 List of the ecological metrics used in this study, their definitions, advantages, and limitations

	Metric	Definition
Community metrics (biomass-weighted)	Biomass-weighted mean and variability of traits	The mean and the variability of trophic level, generality, omnivory, and body size trait values in a community, weighted by species log-transformed biomass (Sonnier et al., 2010). The mean gives indication on the averaged trait values in a community, whereas the variability complements the mean indicator by characterizing the dispersion of the trait values within a community
	Total biomass	Total biomass in the benthic-demersal communities
	Fish/Megabenthos biomass	The log-transformed ratio between the biomass of fish and the biomass of megabenthos in the communities
	Biomass evenness	Measure the evenness in the biomass distribution between species in the community. High values point towards communities with dominating species lower values communities with comparatively well spread biomass between species. Calculated using the Simpson's evenness index
Food web metrics (unweighted)	Number of taxa (TR)	The total number of taxa in the food web, that is, taxa richness. Note that the values of this metric are much lower than the actual number of species because many species are grouped at higher taxonomic level (e.g. sponges, bryozoans, hydroids)
	Number of links (N_{links})	The total number of feeding interactions in the food web
	Link density (LD)	The average number of feeding interactions per taxa, calculated as N_{links}/TR (Dunne et al., 2002)
	Connectance	The proportion of realized feeding links in comparison with all the potential feeding links, and calculated as N_{links}/TR^2 . It characterizes network complexity and is linked to the robustness of food webs to perturbations (Dunne et al., 2002)
	Modularity	Measure whether the food web can be partitioned into distinct groups of interacting species, or modules. Low modularity characterizes food webs that are not organized around distinct groups, whereas high modularity characterizes food web that are highly compartmented (Stouffer & Bascompte, 2011)
	Nestedness	Measure how much the feeding interactions are nested in the food web, for example, a food web is highly nested when specialist consumer diets are subset of generalist diets (Ulrich et al., 2009). High nestedness indicates low trophic complementarity
	Average food web chain length	On average, the minimum number of feeding links between two taxa randomly picked from the food web. It influences community structure and ecosystem functions and is linked to food web robustness to perturbations (Post, 2002)

mean annual conditions, the intra-annual variability and the within-grid cell spatial variability; these variable types allow to describe, respectively, the mean conditions, the seasonality and the habitat heterogeneity experienced by the benthic-demersal fauna. This grouping was done to test whether different community and food web metrics tend to respond to different types of pressure variables. Notably, we expect that the biomass-weighted mean trait values might especially respond to mean pressure values, whereas the variability of the trait values might respond to intra-annual and spatial variability. The mean annual conditions were characterized by average bottom and surface temperature, average chlorophyll-a concentration in sea water during the spring bloom, total number of days with sea ice-cover, average depth, sediment composition and total annual trawling intensity. The intra-annual variability was characterized by monthly variability in bottom and surface temperature, chlorophyll-a concentration and trawling intensity. The within-grid

cell spatial variability was characterized by spatial variability in bottom and surface temperature, depth, chlorophyll-a concentration during the spring bloom and trawling intensity.

Monthly values of bottom and surface temperature data were obtained from the Copernicus product Global reanalysis (PHY_001_030) for the years 2009–2017 on a 0.083×0.083 degree grid. Monthly values of mass concentration of chlorophyll-a in sea water, a proxy for primary productivity, were obtained from the Copernicus product Global ocean biogeochemistry hindcast for the years 2009–2017 on a 0.25×0.25 degree grid. To calculate the annual mean of these variables, we first averaged the monthly values per year and then averaged the annual means in the period 2009–2017. For the primary productivity, we averaged the chlorophyll-a concentration during the spring bloom months only, that is, April–July. To calculate intra-annual variability, we computed the standard deviation of the monthly values per year and then averaged

the standard deviation across the study period. The within-grid cell spatial variability was calculated by computing the spatial standard deviation per month and year and then averaging the standard deviation across the 3 years. Mean depth was calculated based on the bottom-trawl sampling depth and thus match the biological sample locations. Depth variability per grid cell was calculated as the standard deviation of the sampling depth. Ice-cover (number of days with >15% daily sea ice concentration) was extracted for each year at the sampling station from the National Snow and Ice Data Center (Cavalieri et al., 1996), and annual ice-cover was proxied by the average total number of days within a year with ice-cover (Figure 1). Sediment type was extracted at sampling location from seabed sediment maps by Norway's geological survey (contains data under the Norwegian licence for public data [NLOD] made available by Norway's geological survey [NGU]). We used EUNIS sediment hierarchical classification (Davies et al., 2004) and grouped sediment types into seven categories, among which only three were retained in the analysis as they covered a proportion of at least 10% on average across all grid cells, that is, "mixed sediments," "mud, clay and sandy mud" and "sand, muddy sand."

Fisheries can impact benthic-demersal food webs by, for example, reducing the biomass of commercial species or altering megabenthos communities through seabed abrasion (Hiddink et al., 2006; McLaverty et al., 2021; Preciado et al., 2019; Tillin et al., 2006). Here, as we are focusing on benthic-demersal communities, we focus on bottom trawling gears which target bottom-dwelling species and have contact with the seabed. Trawling fishing gears have a more direct impact on the benthic-demersal communities than other gears commonly operating in the area, such as longlines or purse seine, which are assumed to have comparatively a negligible effect on the benthic communities. We used the number of hours of trawling activities in the Barents Sea as a proxy for demersal fishery effort and disturbance on the seabed. Bottom-fishery activities were estimated based on apparent fishing efforts from Global Fishing Watch (globalfishingwatch.org). Satellite-based vessel monitoring system is mandatory on-board for all Norwegian fishing vessels over 15 m (since 2009), and smaller vessels <15 m exempt of AIS are only occurring along the coast. Global Fishing Watch identified fishing vessels and their position using vessels' automatic identification system (AIS) and detect fishing activity using a machine learning algorithm, based, among others, on the vessel speed patterns (Kroodsmas et al., 2018). We downloaded apparent fishing activities on a 1-km² grid (total fishing hours per day per 1-km² cell and per fishing vessel) for the Barents Sea region for the years 2013, 2014 and 2015. We kept only fishing activities from vessels categorized as "trawlers" (including both bottom- and mid-water) and "dredge fishing." To calculate the annual mean, we first summed the fishing hours per year of all selected vessels for each hexagonal grid cell used in this study (see Figure S6) and then we averaged the fishing hours across the 3 years. To calculate the intra-annual variability of trawling, we first summed the trawling hours per month and year, then computed the standard deviation of the monthly values per year and then averaged the standard deviation across the 3 years. The within-grid cell spatial

variability in the trawling was calculated by first summing the fishing hours per year per 1-km², then computing the spatial standard deviation per year and finally averaging the standard deviation across the 3 years. The variables "number of days with ice-cover" and "trawling intensity" were log-transformed due to right-skewed distribution.

2.5 | Statistical analysis

2.5.1 | Cluster analysis of community and food web metrics

To describe the spatial patterns of the benthic-demersal community and food web properties, we clustered the different grid cells to identify groups of grid cells with similar community and food web properties. We clustered the grid cells based on their ecological properties using an archetype analysis (AA, (Cutler & Breiman, 1994). AA focuses on identifying "freak" observations rather than the mean or median observations of a cluster. Here, it identifies grid cells where the benthic-demersal community and food web properties are differing the most. The 18 ecological metrics were normalized (i.e. to a mean of 0 and a variance of 1) before analysis to ensure equal weights in the AA. We tested a range of fixed number of archetypes $k = 1, 2, 3, \dots, 10$, and the residual sum of squares (RSS) of 99 iterations was calculated for each k using the package "archetypes" in R (Eugster & Leisch, 2011). We used the "elbow criterion" to select the optimal number of clusters permitting minimizing the RSS while minimizing the number of archetypes (Figure S7). This is done visually by assessing the number corresponding to a substantial drop in the RSS. Each grid cell is then characterized as a combination of k archetypes instead of being assigned to a specific archetype, that is, each grid cell is characterized by k proportions based on the proximity of the values of the grid cell ecological metrics to the values of the archetypes. Each archetype was exemplified by the grid cell, which resembled the most the archetype (proportion close to 1). We represented the food web at each of these archetype grid cells by displaying taxon biomass, feeding links and taxon groups (fish or megabenthos). For simplicity, we only displayed the taxa that were occurring in more than half of the 100 assembled communities (present in more than 50 communities).

2.5.2 | Response to the environment redundancy analysis

To investigate potential spatial co-variations within, and between, the ecological metrics and the environmental and anthropogenic pressures, we performed a redundancy analysis (RDA). The RDA is a multivariate method that has been shown to give a good overview of community trait response to environmental gradients (Kleyer et al., 2012). The RDA permits assessing linear relationships between two matrices, here between the response matrix of 18

community and food web metrics and the explanatory matrix of 12 environmental and trawling intensity variables. We used a hierarchical partitioning to estimate the importance of each explanatory variable and group of variables (spatial, seasonal, average) and how well they explained the spatial variability of the ecological metrics. Hierarchical partitioning calculates the variable importance from all subset models, leading to an unordered assessment of importance (Lai et al., 2022). All the analyses were performed with the R packages “vegan” and “rdacca.hp” (Lai et al., 2022; Oksanen, 2017).

2.5.3 | Temporal changes per cluster

Finally, we studied whether the benthic-demersal community and food web metrics changed during the period 2009–2017, and whether these changes differed across space. The temporal analysis had to be done on a larger spatial extent than at the grid cell level due to limitations in bottom-trawl samples per year and grid cell. As the archetype analysis identified clusters of grid cells with similar community and food web properties, we calculated temporal changes by aggregating the annual bottom-trawl samples from 5 grid cells for each identified cluster. We selected only 5 grid cells per cluster to keep the same spatial area and to leave a spatial buffer between the different clusters to investigate potential sub-regional temporal dynamics. In 2014, the northern part of the Barents Sea was not sampled, and thus, we excluded 2014 when calculating indices for the clusters located in the northern areas. For each year and cluster, we assembled the benthic-demersal communities and calculated the community and food web properties using the same sampling-randomization method than for the spatial analysis, that is, we assembled 100 random communities based on 10 hauls sampled within the five selected grid cells per cluster, and calculated the ecological metrics on these assembled communities. To relate potential ecological variability to changes in the environmental variables that structure the benthic-demersal communities (variable importance from the RDA analysis), we averaged, across the five selected grid cells per cluster, the time series of bottom and surface temperature at the time of the bottom trawl survey (Aug-Sept) and number of days covered with sea ice. Time series of trawling intensity covering the studied time-period were not available.

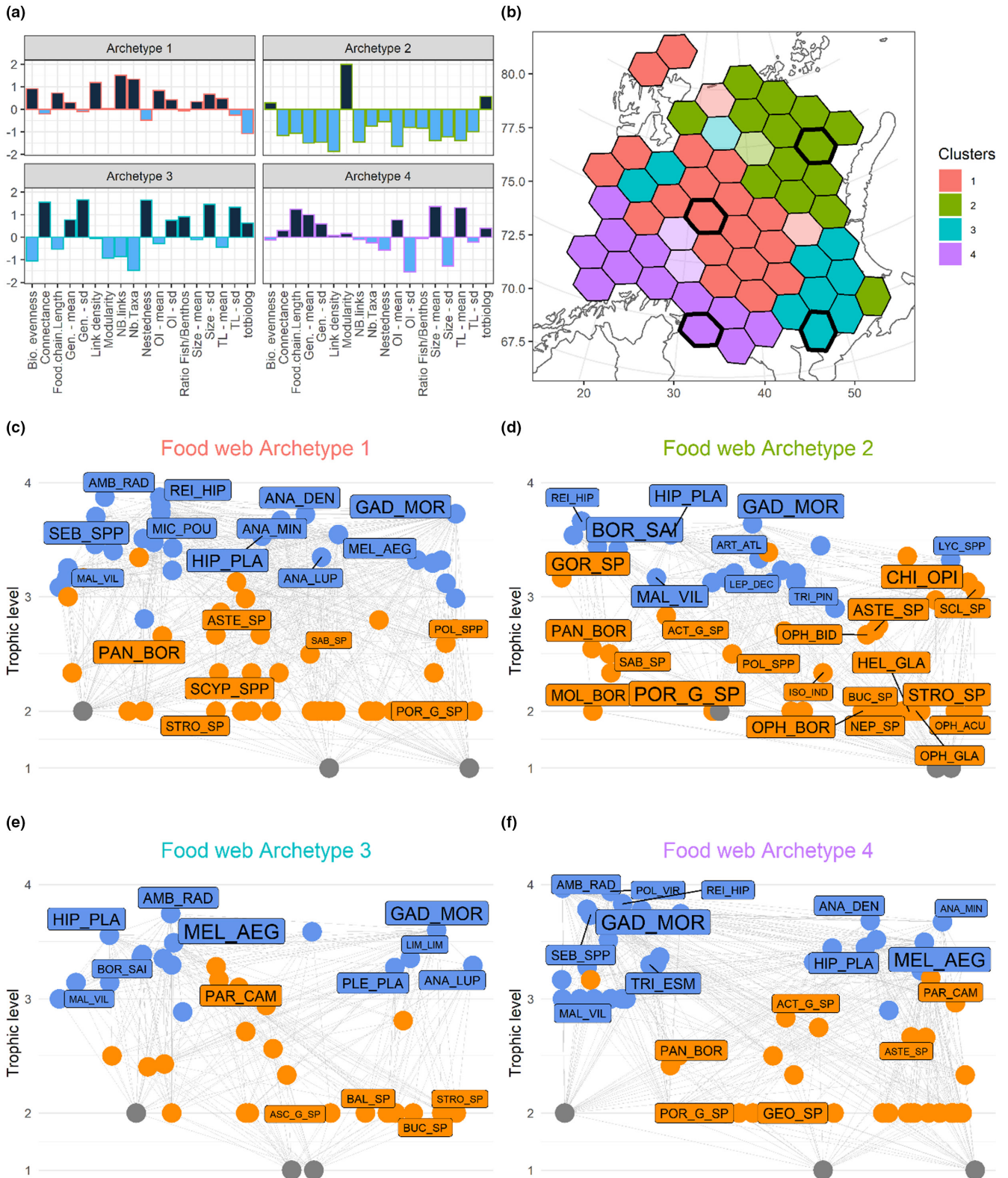
3 | RESULTS

Following the archetype analysis on the ecological metrics, we selected four archetypes as a compromise between the amount of variability explained and complexity (elbow criterion, Figure S7). The clusters associated with the archetypes separate the Barents Sea into four areas: southwest, south-east, central-northwest and northeast (Figure 2b). A first archetype (A1) corresponds to a grid cell in the central Barents Sea. The benthic-demersal communities of this archetype have a high biomass evenness, high biomass-weighted variability in size and omnivory, and low total

biomass, and the food web is characterized by a comparatively high number of feeding links per taxa (Figure 2a). The taxa with the highest biomass in this community were, for fish, the Atlantic cod, the long rough dab *Hippoglossoides platessoides*, and the wolfishes *Anarhichas denticulatus*, *A. minor*, *A. lupus*, and for the megabenthos, the northern shrimp *Pandalus borealis* and starfishes Asteroidea indet. (Figure 2c). A second archetype (A2) corresponds to a grid cell in the northeastern Barents Sea. The food web was characterized by high modularity and low connectance and food chain length. The communities have comparatively low values for all community mean and variability traits (Figure 2a). The community is composed of many benthic species with relatively high biomass, notably sea urchins *Strongylocentrotus* sp., the invasive snow crab *Chionoecetes opilio*, sponges Porifera indet, starfishes and basket stars *Gorgonocephalus* sp. (Figure 2d). The dominating fish species were the Atlantic cod and the polar cod *Boreogadus saida*. A third archetype (A3) is located near the south-eastern coast of the Barents Sea. This archetype food web is characterized by comparatively high connectance, nestedness and a low number of taxa and modularity. The community is characterized by high variability in size, omnivory and TL, and low biomass evenness. The fish species with high biomass in this food web are haddock *Melanogrammus aeglefinus* and Atlantic cod (Figure 2e). The megabenthos biomass is dominated by the invasive red king crab *Paralithodes camtschaticus*. A fourth archetype (A4) corresponds to a coastal grid cell in the center-south Barents Sea. This archetype is characterized by comparatively high mean trophic level and size, low variability in size and omnivory and longer food chain length. The fish species with high biomass in this food web are haddock and Atlantic cod (Figure 2f). The megabenthos with the highest biomass are the northern shrimp, the red king crab and sea anemones *Actinaria* sp, and sponges.

The redundancy analysis of the benthic-demersal community and food web metrics explained 60.9% of the variance. Based on hierarchical partitioning, the variables which explained the highest part of the ecological metrics' spatial variability were annual mean sea surface and bottom temperature, and annual trawling intensity, followed by intra-annual variability in trawling intensity and surface temperature (Figure 3). The variables which represent annual mean conditions were the most important in explaining the variability of the ecological metrics, whereas the variables characterizing the within-cell spatial variability contributed the least to the explained variability (Figure 3).

The loadings and spatial patterns along the first four axes are described, as these axes explained an important part of the variability ($p < .05$). The first axis explains 32.5% of the co-variance and represents a pressure gradient from high mean bottom temperature and high trawling intensity in the southwestern Barents Sea to a long period of ice-covered waters and no or little trawling in the northeastern Barents Sea (Figure 4a,b). The benthic-demersal fauna composition varies along this pressure gradient, with comparatively higher dominance of fish biomass, higher mean size, trophic level and omnivory, higher food chain length and link density and lower



modularity in the southwestern Barents Sea having compared with the northeastern areas.

The second axis explains 17.4% of the variability and separates grid cells in the south-eastern areas characterized by shallow (<100m) depth, sand-dominated sediments and high intra-annual variability in surface and bottom temperature. With the rest of the Barents Sea

(Figure 4a,c), the benthodemersal communities occurring in these south-eastern areas have comparatively high nestedness and connectance, high biomass-weighted variability in taxa' generality and size within the communities, but low modularity and number of taxa.

A third axis explains 11.0% of the variability and distinguishes grid cells in the northwestern and central Barents Sea with

FIGURE 2 Clustering of the benthic-demersal compartment based on the values of their community and food web metrics. (a) Metric values of each archetype. (b) Cluster associated with each grid cell and their spatial distribution. The four grid cells with bold dark contour represent the grid cells, which resemble the most each archetype. (c–f) Representation of the four food webs in each archetype grid cell, only the taxa present in at least 50% of the 100 assembled communities per grid cell are represented. Each dot corresponds to a taxon and the taxon name is labelled using the first three letters of their taxonomic classification, if classified at the species level the first three letters correspond to the genus name and the following three letters to the species name. The dots and labels are coloured orange for megabenthos, blue for fishes and grey for detritus, phytoplankton, and zooplankton. The grey lines represent the documented feeding links between taxa. The taxa are placed on the y-axis based on their trophic level and on the x-axis semi-randomly (grouping species within three clusters based on their shared feeding interactions and an added random value). The size of the taxa labels represents their relative biomass in the benthic-demersal community (small to large represents low to high biomass, respectively). The species with the highest biomass in the archetype food webs are: ACT_G_SP = *Actinaria* sp., ANA_DEN = *Anarhichas denticulatus*, BOR_SAI = *Boreogadus saida*, CHI_OPI = *Chionoecetes opilio*, GAD_MOR = *Gadus morhua*, GEO_SP = *Geodia* sp., GOR_SP = *Gorgonocephalus* sp., HIP_PLA = *Hippoglossoides platessoides*, MAL_VIL = *Mallotus villosus*, MEL_AEG = *Melanogrammus aeglefinus*, PAN_BOR = *Pandalus borealis*, PAR_CAM = *Paralithodes camtschaticus*, PLE_PLA = *Pleuronectes platessa*, POL_VIR = *Pollachius virens*, POR_G_SP = *Porifera* sp., SEB_SPP = *Sebastes* sp., SOM_MIC = *Somniosus microcephalus*, STRO_SP = *Strongylocentrotus* sp., TRI_ESM = *Trisopterus esmarkii*

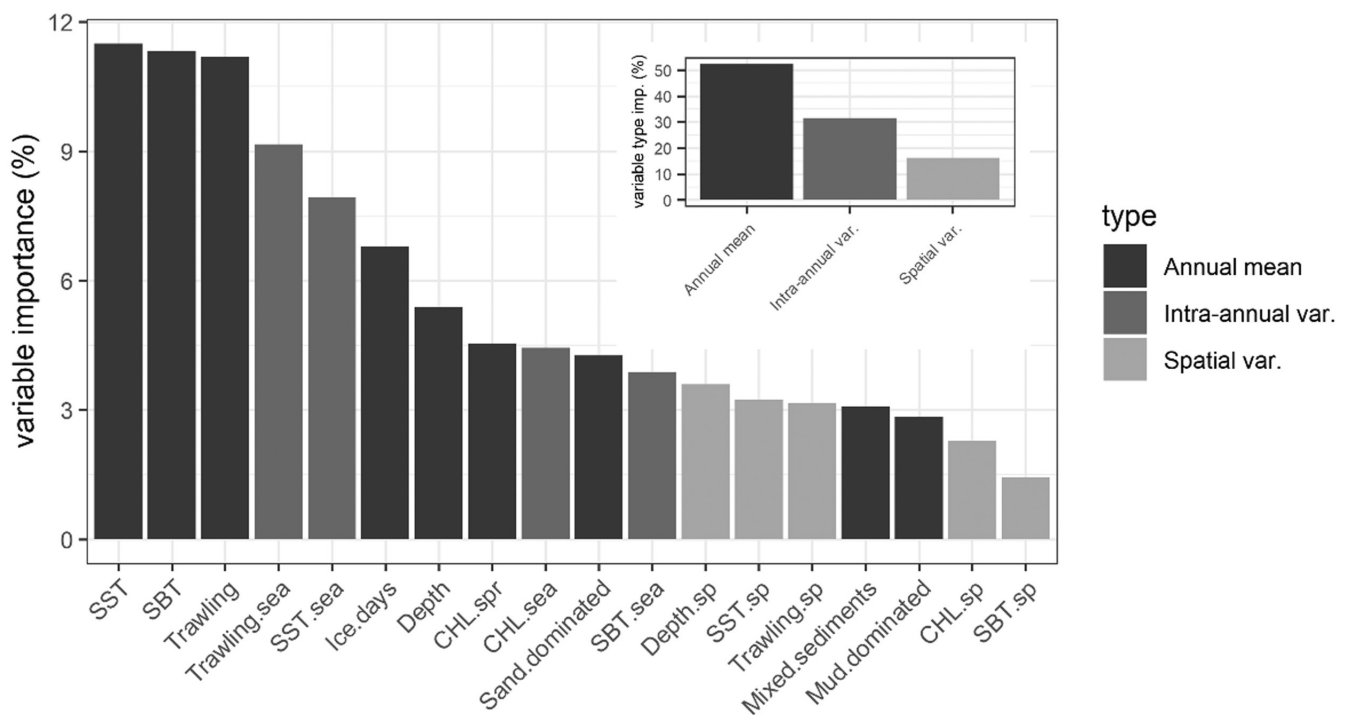


FIGURE 3 Individual importance (%) of the environmental and trawling effort variables to explain the spatial variation in the food web and community metrics, and importance based on the variable type. The explanatory variables are colour-coded based on whether they represent annual mean conditions (black), intra-annual variations (dark grey) or spatial variability within the grid cell (light grey). Variables finishing with “.sp” and “.sea” are variables representing the within-cell spatial variation and intra-annual variation (seasonality), respectively

communities south and north of this central area (Figure 5a,b). The northwestern-central grid cells are characterized by high spatial variability in surface temperature and a higher proportion of mixed sediments, and comparatively high biomass-weighted variability in omnivory and size, and high numbers of taxa and feeding links. A fourth axis explains 5.3% of the remained variance and is characterized by a more heterogeneous spatial pattern, with notable cells in the center-east Barents Sea characterized by high intra-annual variability and mean spring biomass of chlorophyll-a concentration and lower number of days with ice-cover, and higher megabenthos dominance, biomass evenness and biomass-weighted variability in trophic level (Figure 5a,c).

The ecological metrics of the four clusters did not display consistent increasing or decreasing trends during the period 2009–2017, but many metrics displayed large inter-annual variability (Figure 6a–d, for the temporal dynamics of the other metrics see Figure S8). The food web metric modularity remained highest in the northeastern cluster and lowest in the south-eastern cluster (Figure 6a). The nestedness remained relatively highest for the south-eastern cluster throughout the studied period and peaked in 2016 for all clusters but the northeastern one (Figure 6b). Mean body size appeared to decrease in the southwestern, with a peak in 2016, whereas it remained stable for the centre and northeast clusters (Figure 6c). The variability in body size had no specific

trends throughout the period; it remained the lowest for the northeastern cluster and reached similar values in 2016 for the three other clusters, due notably to a dip in the centre and south-western clusters (Figure 6d). The time series of the environmental conditions also displayed high inter-annual variability. Bottom temperature peaked in 2012 and 2016 in all areas, albeit to a lower extent in the northeast cluster, whereas bottom salinity dipped in 2016 in the south-east and peaked in 2010 and 2016 in the south-west. The number of days with ice-cover was abnormally low in 2012 and 2016 for the northeastern cluster.

4 | DISCUSSION

Biogeographical patterns in marine fauna are seldom investigated by integrating across organizational levels and organism groups. Here, for the first time, we integrated spatial patterns in the community composition and food web properties of fish and benthic invertebrates in the Barents Sea and assessed their relations to environmental and fishing pressures. This integration permitted us to obtain a more holistic understanding of how environmental conditions can constrain community composition, which in its turn can influence food web structure. For example, the southwest-northeast gradient in sea bottom temperature and sea ice-cover shapes the community

composition with higher megabenthos biomass and smaller body size in the northeast, which results in a shorter food chain and higher modularity of the food web. We found that the annual mean in the environmental pressures, and notably sea bottom and surface temperature and depth, explained most of the spatial variability in the ecological metrics. However, spatial and temporal variability also co-varied with some ecological metrics. Notably, the variability in body size and omnivory within the community was higher in areas with high spatial heterogeneity in surface temperature. In these areas, located in the central Barents Sea, the Arctic and Atlantic water masses mix. This reveals that more heterogeneous habitats can have higher functional diversity by diversifying the ecological niches available for species.

The common study of benthic-demersal community and food web metrics allowed us to partition the Barents Sea into four sub-regions with similar ecological characteristics, that is, southwest, south-east, northwest-central and northeast sub-regions. The four sub-regions grouping found here based on the benthic-demersal community and food web metrics resembles the grouping based on the taxonomic composition of megabenthos alone (Jørgensen et al., 2015), but there are some notable differences in the groupings found in this study, such as the northwestern cluster that includes the central area (where Atlantic and Arctic water mix) and the more spatially constrained south-eastern cluster. Using various types of metrics at

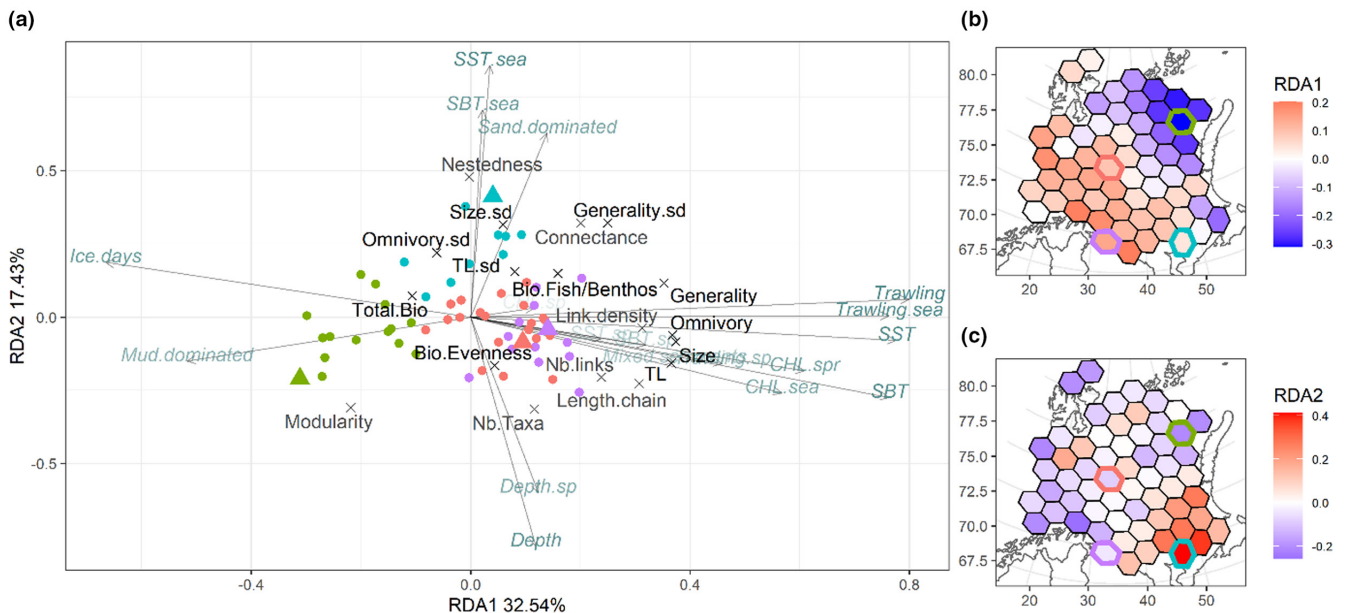


FIGURE 4 Redundancy analysis showing (a) loadings of the benthic-demersal community and food web metrics (grey crosses and labelled in dark for community metrics and grey for food web metrics), the set of environmental variables (grey arrows and italic blue labels), and the grid cell scores (points colour coded based on the archetypal analysis clusters) along the first and second principal axis of the RDA. The spatial pattern of the (b) first and (c) second principal axis of variation. (a) The loading value and orientation of the ecological metrics (grey crosses) show their strength and direction of maximum correlation on the first two principal axis. Metrics that are close to each other are highly correlated and therefore follow similar spatial patterns and have similar response to the environment. Angles between the ecological metrics and the environmental variables represent correlations: small or straight angles (close to 0° or 180°) represent positive or negative linear relationship, respectively, while right angles (90°) express a lack of linear relations. The four grid cells representative of each archetype are depicted as a triangle in the biplot and are geolocalized in the Barents Sea by colouring the grid cell contours in the maps in (b) and (c). SBT05 = average sea bottom temperature at the sampling sites, CHL = chlorophyll-a concentration, icedays = number of days with ice-cover, TL = trophic level, sd = standard deviation, bio = biomass

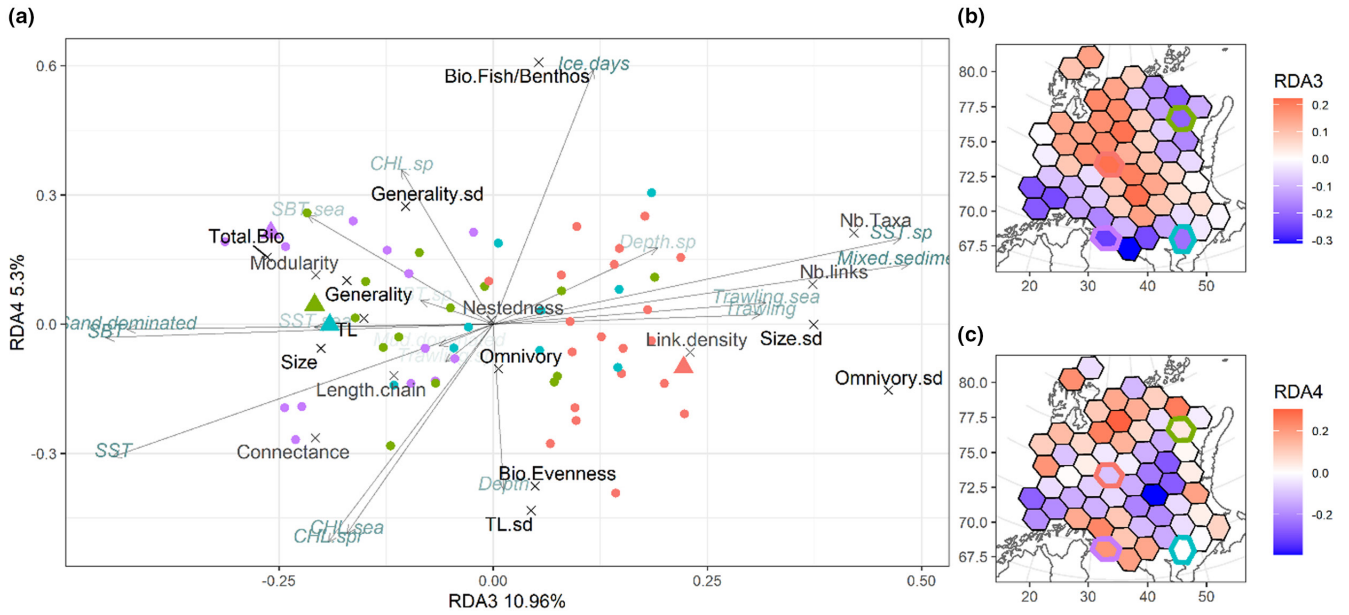


FIGURE 5 Redundancy analysis showing (a) loadings of the bentho-demersal community and food web metrics (grey crosses and labelled in dark for community- and grey for food web metrics), and the set of environmental variables (grey arrows and italics blue labels) along the third and fourth principal axis of the RDA. The spatial pattern of the (b) third and (c) fourth principal axis of variation

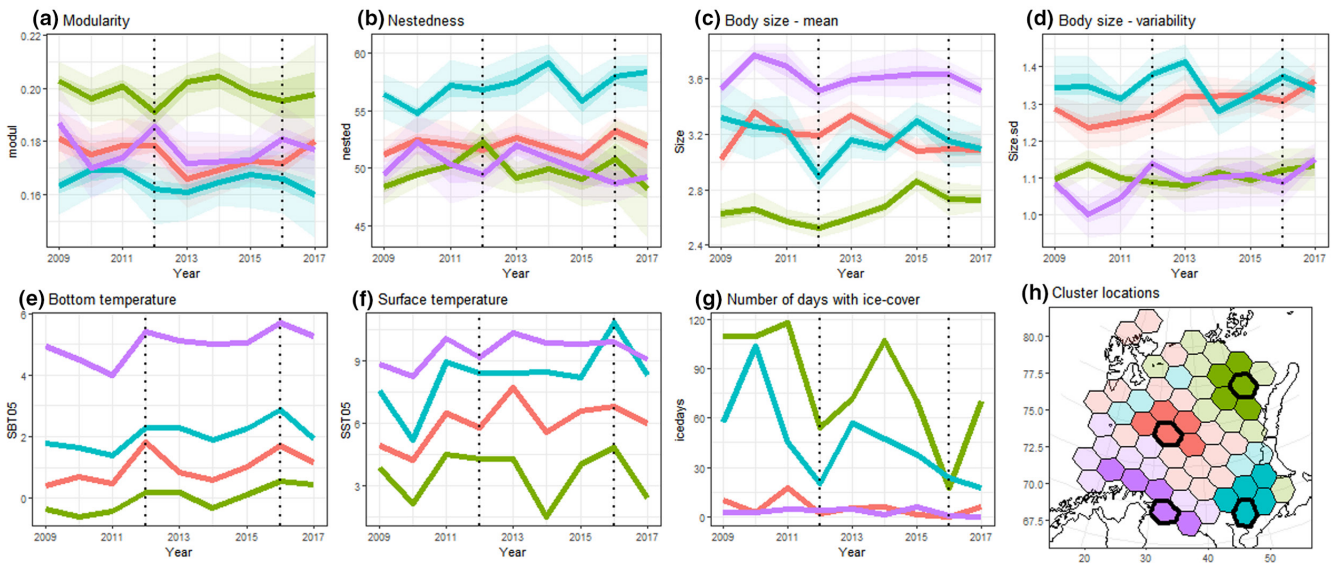


FIGURE 6 Temporal changes of selected unweighted food web (a, b) and biomass-weighted community (c, d) metrics and environmental variables (e-g) for each archetype cluster. Only five grid cells per clusters, including the archetypes, were used to calculate the ecological metrics (grid cells with intense colours in h). (a-d) the bold coloured lines represent the metric' median value. The dark shaded areas represent the 50% credible interval and the light shaded areas the 90% credible interval. The environmental variables (e-g) were calculated as the average value of each cluster's five grid cells. Note that in 2014 no ecological metrics data is available for the two western clusters (red and purple) and that in 2012 the sampling for megabenthos was irregular in the two eastern clusters (green and blue) due to the use of a different gear. The years 2012 and 2016 are highlighted by a vertical dashed line as these years were characterized by extreme environmental conditions in the Barents Sea, with very warm sea bottom temperature and very low ice-cover, as identified in (Husson et al., 2022; Mohamed et al., 2022)

different organizational levels, weighted and unweighted provides complementary information to characterize ecological spatial and temporal patterns (e.g. food web metrics, Kortsch et al., 2021; Olivier et al., 2019). Here, spatial variation in biomass-weighted community traits permitted to distinguish southern communities from northern

communities, whereas presence-based food web properties permitted to distinguish the south-eastern bentho-demersal communities from the rest of the Barents Sea communities.

The Barents Sea is characterized by a strong environmental southwest-northeast gradient linked to warm Atlantic water

entering the southwestern Barents Sea and bringing boreal conditions in the southern areas and to opposite cold Arctic water entering the northeastern Barents Sea and bringing Arctic conditions in the northern areas. Our results showed a similar biogeographical pattern for the benthic-demersal communities: the southwestern area is dominated by boreal species, whereas the northeastern area is dominated by Arctic species with the addition of seasonal migrant boreal species, such as Atlantic cod or capelin *Mallotus villosus*, which migrate northward when the ice retracts (Olsen et al., 2010). In the central area where Atlantic and Arctic water mix, both Arctic and boreal species co-occur. This turnover in taxonomic composition was also documented for demersal fish (Johannesen et al., 2012), benthos (Jørgensen et al., 2015) and their spatial co-variation (Johannesen et al., 2017). The secondary production of Barents Sea megabenthos also follows this spatial pattern, with the highest production in the northeast seasonally ice-covered areas and lowest in the permanently ice-free southwestern areas (Degen et al., 2016). In this study, as expected, the main spatial axis of the variability of the community traits and food web followed also a southwest-northeast gradient. Fish biomass and diversity were, in general, higher in the southwestern communities, whereas benthos biomass and diversity were higher in the northern communities. Community body size, trophic level, omnivory and the food chain length decreased along the southwest-northeast axis. This gradient displays the Arctic-boreal biogeographic divide between communities in the southwestern Barents Sea dominated by boreal species, such as Atlantic cod, haddock, saithe and the large *Geodia* sponge grounds, and the northeast communities dominated by Arctic species, such as polar cod, snow crab, poriferans and Arctic brittle stars. Compared with the Arctic fish species, the boreal fish species are generally larger, more generalist and have a higher trophic level (Wiedmann et al., 2014), which is reflected in these community mean trait values and which also appear to affect the food web structure (co-variation with modularity and food chain length).

Marine food webs are largely structured by taxa traits such as body size (Brose et al., 2019; Pecuchet et al., 2020), the differing trait composition in the Arctic and boreal communities, along with taxa richness, seem to impact the topology of the benthic-demersal food web, with higher modularity in the northeastern Arctic food web and higher food chain length in the southwestern boreal food webs. The Barents Sea Arctic food webs are characterized by high modularity in comparison with the boreal food webs (Kortsch et al., 2019); here, we show that this difference remains when looking only at the benthic-demersal compartment. Modularity and length of the food chain are two food web properties which are hypothesized to affect the resilience of food web to perturbations (Stouffer & Bascompte, 2011), as a perturbation in a modular food web will spread less efficiently through the network. Analysing spatial patterns in food web structure such as modularity and food chain length can permit identifying areas where ecosystems appear more vulnerable to perturbations (i.e. low modularity and short length), and where conservation efforts and mitigation of anthropogenic perturbations could be

prioritized. Among the food web properties singled out for their ecosystem vulnerability implications are connectance, modularity and nestedness. These properties, further discussed below in the Barents Sea context, affect the internal and external stability (i.e. robustness and invasibility) of food webs and are thereby valuable indicators for ecosystem approaches to management and conservation that account for systemic risk (Landi et al., 2018; Levin & Lubchenco, 2008).

The spatial patterns in trait variability within the community permitted distinguished benthic-demersal communities in the northwest, central and south-east Barents Sea to communities north and south of this diagonal. The communities in this area had higher variability in the body size and omnivory values. In addition, the number of taxa and the average number of feeding links per taxa (link density) were, generally, also higher in this cluster. Within this central area of the Barents Sea, the warmer and more saline Atlantic waters mix with the fresher and colder Arctic waters (Oziel et al., 2016). The biological communities are dominated by boreal and Arctic species south and north of this area, respectively (Fossheim et al., 2015). These two communities with different body size and feeding traits overlap in the mix-waters of the central Barents Sea, which is reflected in the increased trait variability observed in these central communities. This shows the importance of studying not only average community trait but also the variability in the trait composition within the community when assessing spatial variation in community composition. Studying the variability can help inform where two ecotypes meet, here boreal and Arctic communities, and can be used as an early-warning signal of ecosystem change (Frainer et al., 2021).

Connectance and nestedness were the highest in the shallow south-eastern communities and co-varied to a certain extent with variability in generality. The combination of higher connectance and higher nestedness implies that there are more realized feeding interactions in these communities and that these interactions tend to overlap across species. The high nestedness and variability in generality indicate that both generalist and specialist species co-occur in these communities and that the diet of the specialist species is a subset of the diet of the generalist species. High nestedness suggests that several taxa share a similar trophic niche, and thus high trophic redundancy in the system. High trophic redundancy is expected to lead to a more resilient food web as the redundancy buffers the ecosystem against species loss caused by external perturbations (Sanders et al., 2018). However, in the case of the south-eastern Barents Sea, the high nestedness is associated with low taxonomic richness and biomass evenness which results in high trophic redundancy but low trophic niche partitioning, that is, low trophic complementarity with few trophic groups (Poisot et al., 2013). Networks with low trophic complementarity might result in non-optimal resource use and can impact ecosystem functions such as consumer biomass production (Poisot et al., 2013). This observed high nestedness and low trophic complementarity might be due to differing environmental conditions linked to less varied topographic and

oceanographic conditions in the area, shallow (less 100m) and sand-dominated sediments, which could limit benthic-demersal community to species with a preference for this habitat, but might also be due to the high biomass of the invasive red king crab in these areas (Anisimova et al., 2005; Falk-Petersen et al., 2011; Oug et al., 2018).

The spread of non-native species in the marine realm is one of the major drivers of ecosystem change with impacts on community dynamics and ecosystem function and services (Molnar et al., 2008; Walsh et al., 2016). The red king crab (*Paralithodes camtschaticus*) and the snow crab (*Chionoecetes opilio*) are invasive species in the Barents Sea. The red king crab was actively introduced in the Barents Sea in the 1960s, and the snow crab was first detected in the Barents Sea in 1996. Currently, both species have reached high biomasses in the ecosystem and are commercially harvested. Here, these two invasive species had large biomasses in two out of the four archetype food webs and reached some of the highest trophic levels among the benthos species. The red king crab is a mainly coastal species and had a relatively high abundance in the south-eastern Barents Sea (Figure 2f), whereas the snow crab is especially present in the central and northeastern Barents Sea (Figure 2c). Both crabs are characterized by having a generalist diet and have a high trophic level in comparison with the other benthic species (Anisimova et al., 2005; Falk-Petersen et al., 2011; Zakharov et al., 2021). These species have impacted the composition of the benthic communities in the invaded areas, with notably reduced biodiversity and benthic biomass (Falk-Petersen et al., 2011) and a turnover in species dominance (Anisimova et al., 2005). The generalist invasive snow crab and red king crab have top-down effects on the benthic communities, as they reduce the biomass of large long-lived species which benefit opportunistic short-lived species (Oug et al., 2018; Pedersen et al., 2018). While it is evident that high snow crab and red king crab biomasses lead to high turnover and reduced biodiversity of benthic species, the implications for ecosystem structure and functioning are still uncertain. To gain a better understanding of their present and future ecosystem impacts as they keep expanding in the Barents Sea, further monitoring and impact assessment of these invasive species is needed (Jørgensen et al., 2015).

The commercial fisheries in the Barents Sea target a few stocks, including Atlantic cod and haddock, and which are caught predominantly using bottom trawls. The trawl fishing activities are located mainly in the southwestern, south-eastern and central areas. Fisheries can have large impacts on benthic-demersal food webs by, for example, reducing the biomass of commercial species and bycatch species, providing additional food sources for benthic scavengers through fisheries waste (Heath et al., 2014) or altering benthic invertebrates communities through seabed abrasion (Hiddink et al., 2006; McLaverty et al., 2021; Tillin et al., 2006). Here, we found that trawling intensity co-varied spatially with multiple ecological metrics. The trawling intensity was higher in areas where the benthic-demersal communities were characterized by higher community-weighted mean trophic level and size

and where the length of the food chain was longer. Yet, this co-variation does not imply causation, as disentangling the effects of environment and fisheries on community and ecosystem structure is a difficult endeavour. Indeed, fishing activities are not randomly distributed but mostly take place in the areas that are accessible (e.g. no ice-cover) and where (and when) specific demersal communities prevail, notably where the biomass of commercial demersal species is the highest and are as such also linked to species seasonal migrations. These species often share similar traits, that is, in the Barents Sea the most fished demersal species are often large predators such as Atlantic cod and haddock. Moreover, fishing pressure and the environment can have cumulative impacts on ecosystems (Coll et al., 2016). Yet, there is large evidence that bottom trawling decrease the overall benthos abundance, biomass and species richness (Hiddink et al., 2020; Sciberras et al., 2018). In the Barents Sea, bottom trawling has been linked to a large decrease in total zoobenthos biomass, by as much as 70% (Denisenko, 2001; Jørgensen et al., 2016). Using a trait-based approach, Jørgensen et al. (2016) estimated the vulnerability to trawling to megabenthos in the Barents Sea and showed that the biomass of species vulnerable to trawling areas was lower in areas with high trawling intensity. Sessile and low mobility biota with longer lifespans such as sponges, soft corals and bivalves took much longer to recover after fishing (>3 years) (Jørgensen et al., 2016; McLaverty et al., 2021; Sciberras et al., 2018). This suggests that trawling in the Barents Sea significantly affects the local taxonomic and functional composition, and biomass of benthic species, which in its turn may have an impact on the structure of the local food web.

There were no clear temporal trends in the ecological metrics in any of the four sub-regions. The absence of temporal trends in the ecological metrics might be due to short-time series (9 years). In addition, the fish communities of the Arctic region of the Barents Sea ecosystem were rapidly transitioning towards more boreal-dominated communities before the start of the study period (before 2009), while during the time series studied here (2009–2017) the pace of borealization lessened (Frainer et al., 2021). Yet, although no trends were apparent, the time series were characterized by high intra-annual variability. Some peaks, or dips, in the ecological metrics were noticeable, but not exclusively, in 2012 and 2016. During 2011–2012 and 2016, the Barents Sea experiences extreme climatic events with marine heatwaves and very low ice-cover (Husson et al., 2022; Mohamed et al., 2022). Several fish populations in the Barents Sea reacted to these extreme years by changing their spatial distribution (Husson et al., 2022). These extreme climatic events might have also impacted the recruitment and survival of early stages of fish and invertebrates. For example, the biomass of 0-group polar cod was very low in 2016 and was nearly absent of its common distribution area in the south-eastern Barents Sea (Eriksen et al., 2020). Here, we show that these displacements during extreme climatic events appear to also affect the community traits and food web properties of the benthic-demersal communities. Although it must be noted that in 2012, the sampling for megabenthos was irregular due

to the use of a different gear on-board the Russian vessel, which might in part influence the 2012 peaks observed in the eastern clusters. The biomass-weighted metrics did not appear to change more than the unweighted food web metrics, with no directional turnover in species and biomass composition in the investigated areas over the last decade, whereas on a longer time-scale large ecological changes have been observed across organism groups (Denisenko, 2001; Eriksen et al., 2017; Fossheim et al., 2015; Fraimer et al., 2017; Leonard & Øien, 2020). Here, the food web metrics were calculated based on the presence/absence of feeding interactions; this unweighted approach does not allow observations of potential changes in the strength of the interactions, whereas it has been shown that considering food web fluxes can give complementary information on the dynamics of an ecosystem (Kortsch et al., 2021).

The ecosystem-based management (EBM) aims to sustainably manage natural resources and biodiversity and minimize impacts on ecosystems, conserving biodiversity and ecosystem functions and services, while balancing social and economic targets. To move towards, EBM requires assessing the states of ecosystem components, their past and future dynamics, and their response to cumulative environmental and anthropogenic pressures. In the marine environment, these pressures include notably climate change, with both long-term trends and increased variability, fisheries and the spread of invasive species (Jørgensen et al., 2019). These pressures can have impacts at the population levels, to community, food web and ecosystem levels. It is, therefore, important to study their impacts across organizational levels. Here, we analysed benthic-demersal communities and food webs turnover along a biogeographical (Arctic-boreal) and pressures spatial gradients. This allowed us to delineate areas where the characteristics of benthic-demersal communities and food webs are similar, and which pressure, or combination of pressures, might have the most impact in these areas (e.g. snow crab and loss of ice-cover in the northeast Barents Sea). Such assessment of ecological indicators and their pressures is needed to prioritize conservation efforts. The Barents Sea is warming at a rate exceeding the global average, and the ice-cover extent is diminishing (Ingvaldsen et al., 2021), which may cause the expansion of invasive and boreal species and the fisheries that target them into these fragile ecosystems (Fauchald et al., 2021). These concerns caused the Norwegian Government to tentatively close the high north areas of the Barents Sea for trawling (Jørgensen et al., 2020). This illustrates the importance of taking management measures that mitigate the cumulative impacts of environmental and anthropogenic pressures on the Arctic communities and food webs (e.g. marine protected areas, fishing gears restrictions) and continuous monitoring of ecosystem states. This study focused on the benthic compartment and assessed mainly feeding traits and interactions; future analyses should include other compartments (e.g., pelagic) and ecological indicators and pressures to study cumulative impacts on ecosystem functioning and services.

ACKNOWLEDGEMENTS

This study is part of the BSECO project funded by Arktis 2030 (BSECO Barentshavet i endring Contract nr. QZA-15/0137) and the BarentsRisk project, assessing risks of cumulative impacts on the Barents Sea ecosystem and its services, funded by Research Council of Norway BarentsRisk (proj #288192). We are grateful to all the people working on the joint ecosystem surveys at the Institute of Marine Research (IMR), Norway, and Polar Branch of the Russian Federal Research Institute of Fisheries and Oceanography (PINRO), Russia.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The food web, species traits, and ecological metrics datasets as well as the Rcode to reproduce the figures are available on github.com/LaurenePecuchet/Barents_ComFW

ORCID

Laurene Pecuchet  <https://orcid.org/0000-0002-8930-8786>

REFERENCES

- Albouy, C., Archambault, P., Appeltans, W., Araújo, M. B., Beauchesne, D., Cazelles, K., Cirtwill, A. R., Fortin, M. J., Galiana, N., Leroux, S. J., Pellissier, L., Poisot, T., Stouffer, D. B., Wood, S. A., & Gravel, D. (2019). The marine fish food web is globally connected. *Nature Ecology and Evolution*, 3(8), 1153–1161. <https://doi.org/10.1038/s41559-019-0950-y>
- Anisimova, N., Berenboim, B., Gerasimova, O., Manushin, I., & Pinchukov, M. (2005). On the effect of red king crab on some components of the Barents Sea ecosystem.
- Barnes, R., Sahr, K., Evenden, G., Johnson, A., & Warmerdam, F. (2018). dggridR: Discrete global grids for R.
- Beukhof, E., Frelat, R., Pecuchet, L., Maureaud, A., Dencker, T. S., Sölmundsson, J., Punzón, A., Primicerio, R., Hidalgo, M., Möllmann, C., & Lindegren, M. (2019). Marine fish traits follow fast-slow continuum across oceans. *Scientific Reports*, 9(1), 17878. <https://doi.org/10.1038/s41598-019-53998-2>
- Blowes, S. A., Supp, S. R., Antão, L. H., Bates, A., Bruelheide, H., Chase, J. M., Moyes, F., Magurran, A., McGill, B., Myers-Smith, I. H., Winter, M., Bjorkman, A. D., Bowler, D. E., Byrnes, J. E. K., Gonzalez, A., Hines, J., Isbell, F., Jones, H. P., Navarro, L. M., ... Dornelas, M. (2019). The geography of biodiversity change in marine and terrestrial assemblages. *Science*, 366(6463), 339–345. <https://doi.org/10.1126/science.aaw1620>
- Brose, U., Archambault, P., Barnes, A. D., Bersier, L. F., Boy, T., Canning-Clode, J., Conti, E., Dias, M., Digel, C., Dissanayake, A., Flores, A. A. V., Fussmann, K., Gauzens, B., Gray, C., Häussler, J., Hirt, M. R., Jacob, U., Jochum, M., Kéfi, S., ... Iles, A. C. (2019). Predator traits determine food-web architecture across ecosystems. *Nature Ecology and Evolution*, 3(6), 919–927. <https://doi.org/10.1038/s41559-019-0899-x>
- Cavaliere, D. J., Parkinson, C. L., Gloersen, P., & Zwally, H. J. (1996). *Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave data, version 1*. NASA National Snow and Ice Data Center Distributed Active Archive Center.
- Chase, J. M., & Leibold, M. A. (2003). *Ecological niches*. University of Chicago Press.

- Coll, M., Steenbeek, J., Sole, J., Palomera, I., & Christensen, V. (2016). Modelling the cumulative spatial-temporal effects of environmental drivers and fishing in a NW Mediterranean marine ecosystem. *Ecological Modelling*, 331, 100–114. <https://doi.org/10.1016/j.ecolmodel.2016.03.020>
- Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *Inter Journal, Complex Systems (1965)*, 5, 1–9.
- Cutler, A., & Breiman, L. (1994). Archetypal analysis. *Technometrics*, 36(4), 338. <https://doi.org/10.2307/1269949>
- Davies, C. E., Moss, D., & Hill, M. O. (2004). Eunis Habitat Classification Revised 2004, 311.
- Degen, R., Jørgensen, L. L., Ljubin, P., Ellingsen, I. H., Pehlke, H., & Brey, T. (2016). Patterns and drivers of megabenthic secondary production on the Barents Sea shelf. *Marine Ecology Progress Series*, 546, 1–16. <https://doi.org/10.3354/meps11662>
- Delmas, E., Besson, M., Brice, M. H., Burkle, L. A., Dalla Riva, G. V., Fortin, M. J., Gravel, D., Guimarães, P. R., Jr., Hembray, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., & Poisot, T. (2019). Analysing ecological networks of species interactions. *Biological Reviews*, 94(1), 16–36. <https://doi.org/10.1111/brv.12433>
- Denisenko, S. G. (2001). Long-term changes of zoobenthos biomass in the Barents Sea. *Proceedings of the Zoological Institute of the Russian Academy of Sciences*, 289, 59–66.
- Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*, 99(20), 12917–12922. <https://doi.org/10.1073/pnas.192407699>
- Dunne, J. A., Williams, R. J., & Martinez, N. D. (2004). Network structure and robustness of marine food webs. *Marine Ecology Progress Series*, 273, 291–302. <https://doi.org/10.3354/meps273291>
- Eriksen, E., Bagøien, E., Strand, E., Primicerio, R., Prokhorova, T., Trofimov, A., & Prokopchuk, I. (2020). The record-warm Barents Sea and 0-group fish response to abnormal conditions. *Frontiers in Marine Science*, 7, 338. <https://doi.org/10.3389/fmars.2020.00338>
- Eriksen, E., Gjøsæter, H., Prozorkevich, D., Shamray, E., Dolgov, A., Skern-Mauritzen, M., Stiansen, J. E., Kovalev, Y., & Sunnanå, K. (2018). From single species surveys towards monitoring of the Barents Sea ecosystem. *Progress in Oceanography*, 166, 4–14. <https://doi.org/10.1016/j.pocean.2017.09.007>
- Eriksen, E., Skjoldal, H. R., Dolgov, A. V., Strand, E., Keulder-Stenevik, F., Prokopchuk, I. P., Prokopchuk, T. A., Prozorkevich, D., & Benzik, A. N. (2021). Diet and trophic structure of fishes in the Barents Sea: Seasonal and spatial variations. *Progress in Oceanography*, 197, 102663. <https://doi.org/10.1016/j.pocean.2021.102663>
- Eriksen, E., Skjoldal, H. R., Gjøsæter, H., & Primicerio, R. (2017). Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Progress in Oceanography*, 151, 206–226. <https://doi.org/10.1016/j.pocean.2016.12.009>
- Eugster, M. J. A., & Leisch, F. (2011). Weighted and robust archetypal analysis. *Computational Statistics and Data Analysis*, 55(3), 1215–1225. <https://doi.org/10.1016/j.csda.2010.10.017>
- Falk-Petersen, J., Renaud, P., & Anisimova, N. (2011). Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea—a review. *ICES Journal of Marine Science*, 68(3), 479–488. <https://doi.org/10.1093/icesjms/fsq192>
- Fauchald, P., Arneberg, P., Debernard, J. B., Lind, S., Olsen, E., & Hausner, V. H. (2021). Poleward shifts in marine fisheries under Arctic warming. *Environmental Research Letters*, 16(7), 74057. <https://doi.org/10.1088/1748-9326/ac1010>
- 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 Climate Change*, 5(7), 673–677. <https://doi.org/10.1038/nclimate2647>
- Frainer, A., Primicerio, R., Dolgov, A., Fossheim, M., Johannesen, E., Lind, S., & Aschan, M. (2021). Increased functional diversity warns of ecological transition in the Arctic. *Proceedings of the Royal Society B: Biological Sciences*, 288, 20210054. <https://doi.org/10.1098/rspb.2021.0054>
- Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., & Aschan, M. M. (2017). Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences of the United States of America*, 114(46), 12202–12207. <https://doi.org/10.1073/pnas.1706080114>
- Frelat, R., Kortsch, S., Kröncke, I., Neumann, H., Nordström, M. C., Olivier, P. E. N., & Sell, A. F. (2022). Food web structure and community composition: A comparison across space and time in the North Sea. *Ecography*, 2022(2). <https://doi.org/10.1111/ecog.05945>
- Gauzens, B., Barnes, A., Giling, D. P., Hines, J., Jochum, M., Lefcheck, J. S., Rosenbaum, B., Wang, S., & Brose, U. (2019). Fluxweb: An R package to easily estimate energy fluxes in food webs. *Methods in Ecology and Evolution*, 10(2), 270–279. <https://doi.org/10.1111/2041-210X.13109>
- Gravel, D., Albouy, C., & Thuiller, W. (2016). The meaning of functional trait composition of food webs for ecosystem functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1694), 20150268. <https://doi.org/10.1098/rstb.2015.0268>
- Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E. H., Høines, Å. S., Hoel, A. H., Ingvaldsen, R. B., Jørgensen, L. L., Knutsen, T., Loeng, H., Naustvoll, L. J., Rottingen, I., & Sunnanå, K. (2017). Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents seas: A review of possibilities and constraints. *Fisheries Research*, 188, 38–57. <https://doi.org/10.1016/j.fishres.2016.12.002>
- Heath, M. R., Cook, R. M., Cameron, A. I., Morris, D. J., & Speirs, D. C. (2014). Cascading ecological effects of eliminating fishery discards. *Nature Communications*, 5(1), 3893. <https://doi.org/10.1038/ncomms4893>
- Hiddink, J. G., Kaiser, M. J., Sciberras, M., McConnaughey, R. A., Mazar, T., Hilborn, R., Collie, J. S., Roland Pitcher, C., Parma, A. M., Suuronen, P., Rijnsdorp, A. D., & Jennings, S. (2020). Selection of indicators for assessing and managing the impacts of bottom trawling on seabed habitats. *Journal of Applied Ecology*, 57(7), 1199–1209. <https://doi.org/10.1111/1365-2664.13617>
- Hiddink, J. G., Jennings, S., Kaiser, M. J., Queirós, A. M., Duplisea, D. E., & Piet, G. J. (2006). Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(4), 721–736. <https://doi.org/10.1139/f05-266>
- Husson, B., Lind, S., Fossheim, M., Kato-Solvang, H., Skern-Mauritzen, M., Pécuchet, L., Ingvaldsen, R. B., Dolgov, A. V., & Primicerio, R. (2022). Successive extreme climatic events lead to immediate, large-scale, and diverse responses from fish in the Arctic. *Global Change Biology*, 28, 3728–3744. <https://doi.org/10.1111/gcb.16153>
- ICES (2019). Barents Sea Ecoregion – Ecosystem overview. In Report of the ICES Advisory Committee, 2019. ICES Advice 2019, Section 5.1, (May), 12. <https://doi.org/10.17895/ices.advice.5747>
- Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V., & Dolgov, A. V. (2021). Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth &*

- Environment*, 2, 874–889. <https://doi.org/10.1038/s43017-021-00228-x>
- Johannesen, E., Høines, Å. S., Dolgov, A. V., & Fossheim, M. (2012). Demersal fish assemblages and spatial diversity patterns in the arctic-Atlantic transition zone in the barents sea. *PLoS One*, 7(4), e34924. <https://doi.org/10.1371/journal.pone.0034924>
- Johannesen, E., Jørgensen, L. L., Fossheim, M., Primicerio, R., Greenacre, M., Ljubin, P. A., Dolgov, A. V., Ingvaldsen, R. B., Anisimova, N. A., & Manushin, I. E. (2017). Large-scale patterns in community structure of benthos and fish in the Barents Sea. *Polar Biology*, 40(2), 237–246. <https://doi.org/10.1007/s00300-0-016-1946-6>
- Jørgensen, L. L., Bakke, G., & Hoel, A. H. (2020). Responding to global warming: New fisheries management measures in the Arctic. *Progress in Oceanography*, 188, 102423. <https://doi.org/10.1016/j.pocean.2020.102423>
- Jørgensen, L. L., Planque, B., Thangstad, T. H., & Certain, G. (2016). Vulnerability of megabenthic species to trawling in the Barents Sea. *ICES Journal of Marine Science*, 73(suppl_1), i84–i97. <https://doi.org/10.1093/icesjms/fsv107>
- Jørgensen, L. L., Ljubin, P., Skjoldal, H. R., Ingvaldsen, R. B., Anisimova, N., & Manushin, I. (2015). Distribution of benthic megafauna in the Barents Sea: Baseline for an ecosystem approach to management. *ICES Journal of Marine Science*, 72(2), 595–613. <https://doi.org/10.1093/icesjms/fsu106>
- Jørgensen, L. L., Logerwell, E. A., Strelkova, N., Zakharov, D., Roy, V., Nozères, C., Bluhm, B. A., Olafsdottir, S. H., Burgos, J. M., Sorensen, J., Zimina, O., & Rand, K. (2022). International megabenthic long-term monitoring of a changing arctic ecosystem: Baseline results. *Progress in Oceanography*, 200, 102712. <https://doi.org/10.1016/j.pocean.2021.102712>
- Jørgensen, L. L., Primicerio, R., Ingvaldsen, R., Fossheim, M., Strelkova, N., Thangstad, T., Manushin, I., & Zakharov, D. (2019). Impact of multiple stressors on sea bed fauna in a warming Arctic. *Marine Ecology Progress Series*, 608, 1–12. <https://doi.org/10.3354/meps12803>
- Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, 3(2), 157–164. <https://doi.org/10.2307/3235676>
- Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R. J., Strauss, B., Thuiller, W., & Lavorel, S. (2012). Assessing species and community functional responses to environmental gradients: Which multivariate methods? *Journal of Vegetation Science*, 23(5), 805–821. <https://doi.org/10.1111/j.1654-1103.2012.01402.x>
- Kones, J. K., Soetaert, K., van Oevelen, D., & Owino, J. O. (2009). Are network indices robust indicators of food web functioning? A Monte Carlo approach. *Ecological Modelling*, 220(3), 370–382. <https://doi.org/10.1016/j.ecolmodel.2008.10.012>
- Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, 282(1814), 20151546. <https://doi.org/10.1098/rspb.2015.1546>
- Kortsch, S., Frelat, R., Pecuchet, L., Olivier, P., Putnis, I., Bonsdorff, E., Ojaveer, H., Jurgensone, I., Stråke, S., Rubene, G., Krüze, E., & Nordström, M. C. (2021). Disentangling temporal food web dynamics facilitates understanding of ecosystem functioning. *Journal of Animal Ecology*, 90(5), 1205–1216. <https://doi.org/10.1111/1365-2656.13447>
- Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A. V., & Planque, B. (2019). Food-web structure varies along environmental gradients in a high-latitude marine ecosystem. *Ecography*, 42(2), 295–308. <https://doi.org/10.1111/ecog.03443>
- Kroodsma, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., Wilson, A., Bergman, B., White, T. D., Block, B. A., Woods, P., Sullivan, B., Costello, C., & Worm, B. (2018). Tracking the global footprint of fisheries. *Science*, 359(6378), 904–908. <https://doi.org/10.1126/SCIENCE.AAO5646>
- Lai, J., Zou, Y., Zhang, J., & Peres-Neto, P. R. (2022). Generalizing hierarchical and variation partitioning in multiple regression and canonical analyses using the rdacca.Hp R package. *Methods in Ecology and Evolution*, 13, 782–788. <https://doi.org/10.1111/2041-210X.13800>
- Laigle, I., Aubin, I., Digel, C., Brose, U., Boulangeat, I., & Gravel, D. (2018). Species traits as drivers of food web structure. *Oikos*, 127(2), 316–326. <https://doi.org/10.1111/oik.04712>
- Landi, P., Minoarivelo, H. O., Brännström, Å., Hui, C., & Dieckmann, U. (2018). Complexity and stability of ecological networks: A review of the theory. *Population Ecology*, 60(4), 319–345. <https://doi.org/10.1007/s10144-018-0628-3>
- Leonard, D., & Øien, N. (2020). Estimated abundances of cetacean species in the Northeast Atlantic from two multiyear surveys conducted by Norwegian vessels between 2002–2013. *NAMMCO Scientific Publications*, 11. <https://doi.org/10.7557/3.4695>
- Levin, S. A., & Lubchenco, J. (2008). Resilience, robustness, and marine ecosystem-based management. *Bioscience*, 58(1), 27–32. <https://doi.org/10.1641/B580107>
- Lind, S., Ingvaldsen, R. B., & Furevik, T. (2018). Arctic warming hotspot in the northern Barents Sea linked to declining sea-ice import. *Nature Climate Change*, 8(7), 634–639. <https://doi.org/10.1038/s41558-018-0205-y>
- Magurran, A. E., Dornelas, M., Moyes, F., Gotelli, N. J., & McGill, B. (2015). Rapid biotic homogenization of marine fish assemblages. *Nature Communications*, 6, 1–5. <https://doi.org/10.1038/ncomm59405>
- McLaverly, C., Dinesen, G., Gislason, H., Brooks, M., & Eigaard, O. (2021). Biological traits of benthic macrofauna show sizebased differences in response to bottom trawling intensity. *Marine Ecology Progress Series*, 671, 1–19. <https://doi.org/10.3354/meps13790>
- Mindel, B. L., Neat, F. C., Trueman, C. N., Webb, T. J., & Blanchard, J. L. (2016). Functional, size and taxonomic diversity of fish along a depth gradient in the deep sea. *PeerJ*, 2016(9), 1–25. <https://doi.org/10.7717/peerj.2387>
- Mindel, B. L., Webb, T. J., Neat, F. C., & Blanchard, J. L. (2016). A trait-based metric sheds new light on the nature of the body size-depth relationship in the deep sea. *Journal of Animal Ecology*, 85(2), 427–436. <https://doi.org/10.1111/1365-2656.12471>
- Mohamed, B., Nilsen, F., & Skogseth, R. (2022). Marine heatwaves characteristics in the Barents Sea based on high resolution satellite data (1982–2020). *Frontiers in Marine Science*, 9, 4436. <https://doi.org/10.3389/fmars.2022.821646>
- Molnar, J. L., Gamboa, R. L., Revenga, C., & Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6(9), 485–492. <https://doi.org/10.1890/070064>
- Mouillot, D., Dumay, O., & Tomasini, J. A. (2007). Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Estuarine, Coastal and Shelf Science*, 71(3–4), 443–456. <https://doi.org/10.1016/j.ecss.2006.08.022>
- Oksanen, J. (2017). *Vegan: ecological diversity*. R Package Version 2.4–4, 11. Retrieved from <https://cran.r-project.org/package=vegan>
- Olesen, J. M., Stefanescu, C., & Traveset, A. (2011). Strong, long-term temporal dynamics of an ecological network. *PLoS One*, 6(11), e26455. <https://doi.org/10.1371/journal.pone.0026455>
- Olivier, P., Frelat, R., Bonsdorff, E., Kortsch, S., Kröncke, I., Möllmann, C., Neumann, H., Sell, A. F., & Nordström, M. C. (2019). Exploring the temporal variability of a food web using long-term biomonitoring

- data. *Ecography*, 42(12), 2107–2121. <https://doi.org/10.1111/ecog.04461>
- Olsen, E., Aanes, S., Mehl, S., Holst, J. C., Aglen, A., & Gjøsæter, H. (2010). Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: A review of the biological value of the area. *ICES Journal of Marine Science*, 67(1), 87–101. <https://doi.org/10.1093/icesjms/fsp229>
- Oug, E., Sundet, J. H., & Cochrane, S. K. J. (2018). Structural and functional changes of soft-bottom ecosystems in northern fjords invaded by the red king crab (*Paralithodes camtschaticus*). *Journal of Marine Systems*, 180, 255–264. <https://doi.org/10.1016/j.jmarsys.2017.07.005>
- Oziel, L., Sirven, J., & Gascard, J.-C. (2016). The Barents Sea frontal zones and water masses variability (1980–2011). *Ocean Science*, 12(1), 169–184. <https://doi.org/10.5194/os-12-169-2016>
- Pecuchet, L., Blanchet, M.-A., Frainer, A., Husson, B., Jørgensen, L. L., Kortsch, S., & Primicerio, R. (2020). Novel feeding interactions amplify the impact of species redistribution on an Arctic food web. *Global Change Biology*, 26(9), 4894–4906. <https://doi.org/10.1111/gcb.15196>
- Pecuchet, L., Reygondeau, G., Cheung, W. W. L., Licandro, P., van Denderen, P. D., Payne, M. R., & Lindegren, M. (2018). Spatial distribution of life-history traits and their response to environmental gradients across multiple marine taxa. *Ecosphere*, 9(10), e02460. <https://doi.org/10.1002/ecs2.2460>
- Pecuchet, L., Törnroos, A., & Lindegren, M. (2016). Patterns and drivers of fish community assembly in a large marine ecosystem. *Marine Ecology Progress Series*, 546, 239–248. <https://doi.org/10.3354/meps11613>
- Pedersen, T., Fuhrmann, M. M., Lindstrøm, U., Nilssen, E. M., Ivarjord, T., Ramasco, V., Jørgensen, L. L., Sundet, J. H., Sivertsen, K., Källgren, E., Hjelset, A. M., Michaelsen, C., Systad, G., Norrbin, F., Svenning, M.-A., Bjørge, A., Steen, H., & Nilssen, K. T. (2018). Ecosystem structure and trophic control in an Atlantic fjord invaded by the red king crab. *Marine Ecology Progress Series*, 596, 13–31.
- Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M. A., Melián, C. J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N. E., & Gravel, D. (2018). Comparing species interaction networks along environmental gradients. *Biological Reviews*, 93(2), 785–800. <https://doi.org/10.1111/brv.12366>
- Planque, B., Primicerio, R., Michalsen, K., Aschan, M., Certain, G., Dalpadado, P., Gjoseater, 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. *Ecology*, 95(5), 1430. <https://doi.org/10.1890/13-1062.1>
- Poisot, T., Mouquet, N., & Gravel, D. (2013). Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. *Ecology Letters*, 16(7), 853–861. <https://doi.org/10.1111/ele.12118>
- Post, D. M. (2002). The long and short of food-chain length. *Trends in Ecology & Evolution*, 17(6), 269–277. [https://doi.org/10.1016/S0169-5347\(02\)02455-2](https://doi.org/10.1016/S0169-5347(02)02455-2)
- Preciado, I., Arroyo, N. L., González-Irusta, J. M., López-López, L., Punzón, A., Muñoz, I., & Serrano, A. (2019). Small-scale spatial variations of trawling impact on food web structure. *Ecological Indicators*, 98, 442–452. <https://doi.org/10.1016/j.ecolind.2018.11.024>
- Sanders, D., Thébault, E., Kehoe, R., & Frank van Veen, F. J. (2018). Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences of the United States of America*, 115(10), 2419–2424. <https://doi.org/10.1073/pnas.1716825115>
- Sciberras, M., Hiddink, J. G., Jennings, S., Szostek, C. L., Hughes, K. M., Kneafsey, B., Clarke, L. J., Ellis, N., Rijnsdorp, A. D., McConnaughey, R. A., Hilborn, R., Collie, J. S., Roland Pitcher, C., Amoroso, R. O., Parma, A. M., Suuronen, P., & Kaiser, M. J. (2018). Response of benthic fauna to experimental bottom fishing: A global meta-analysis. *Fish and Fisheries*, 19(4), 698–715. <https://doi.org/10.1111/faf.12283>
- Smedsrud, L. H., Esau, I., Ingvaldsen, R. B., Eldevik, T., Haugan, P. M., Li, C., Lien, V. S., Olsen, A., Omar, A. M., Ottera, O. H., Risebrobakken, B., Sando, A. B., Semenov, V. A., & Sorokina, S. A. (2013). The role of the Barents Sea in the Arctic climate system. *Reviews of Geophysics*, 51(3), 415–449. <https://doi.org/10.1002/rog.20017>
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10(12), 1115–1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- Soininen, J., Heino, J., & Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, 27(1), 96–109. <https://doi.org/10.1111/geb.12660>
- Sonnier, G., Shipley, B., & Navas, M. L. (2010). Quantifying relationships between traits and explicitly measured gradients of stress and disturbance in early successional plant communities. *Journal of Vegetation Science*, 21(6), 1014–1024. <https://doi.org/10.1111/j.1654-1103.2010.01210.x>
- Stouffer, D. B., & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences of the United States of America*, 108(9), 3648–3652. <https://doi.org/10.1073/pnas.1014353108>
- Tillin, H. M., Hiddink, J. G., Jennings, S., & Kaiser, M. J. (2006). Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*, 318, 31–45. <https://doi.org/10.3354/meps318031>
- Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, 48, 25–48. <https://doi.org/10.1146/annurev-ecolsys-110316>
- Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos*, 118(1), 3–17. <https://doi.org/10.1111/j.1600-0706.2008.17053.x>
- van Putten, I. E., Kulmala, S., Thébaud, O., Dowling, N., Hamon, K. G., Hutton, T., & Pascoe, S. (2012). Theories and behavioural drivers underlying fleet dynamics models. *Fish and Fisheries*, 13(2), 216–235. <https://doi.org/10.1111/j.1467-2979.2011.00430.x>
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5), 882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Walsh, J. R., Carpenter, S. R., & Vander Zanden, M. J. (2016). Invasive species triggers a massive loss of ecosystem services through a trophic cascade. *Proceedings of the National Academy of Sciences of the United States of America*, 113(15), 4081–4085. <https://doi.org/10.1073/pnas.1600366113>
- Wiedmann, M. A., Primicerio, R., Dolgov, A., Ottesen, C. A. M., & Aschan, M. (2014). Life history variation in barents sea fish: Implications for sensitivity to fishing in a changing environment. *Ecology and Evolution*, 4(18), 3596–3611. <https://doi.org/10.1002/ece3.1203>
- Yodzis, P., & Winemiller, K. O. (1999). In search of operational Trophospecies in a tropical aquatic food web. *Oikos*, 87(2), 327. <https://doi.org/10.2307/3546748>
- Zakharov, D. V., Manushin, I. E., Nosova, T. B., Strelkova, N. A., & Pavlov, V. A. (2021). Diet of snow crab in the Barents Sea and macrozoobenthic communities in its area of distribution. *ICES Journal of Marine Science*, 78(2), 545–556. <https://doi.org/10.1093/icesjms/fsaa132>

Zuur, A. F., Ieno, E. N., & Smith, G. M. (2007). *Analysing ecological data* (Vol. 680). Springer.

BIOSKETCH

Laurene Pecuchet is an associate professor in fisheries biology at The Arctic University of Norway (UiT). She studies the impacts of global change on marine ecosystems, from fish populations to food web, by combining empirical analysis of scientific surveys, trait-based approach and modelling tools.

Author Contributions: L.P. conceived the ideas with input from all authors. L.P., L.J., B.H., E.E., A.D. provided data. L.P. performed the analyses. L.P. wrote the manuscript with input from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Pecuchet, L., Jørgensen, L. L., Dolgov, A. V., Eriksen, E., Husson, B., Skern-Mauritzen, M., & Primicerio, R. (2022). Spatio-temporal turnover and drivers of benthic-demersal community and food web structure in a high-latitude marine ecosystem. *Diversity and Distributions*, 00, 1–18. <https://doi.org/10.1111/ddi.13580>