



Benthic transition zones in the Atlantic gateway to a changing Arctic ocean

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ABSTRACT

The biogeographic transition from boreal to Arctic marine communities entails a strong taxonomic and functional turnover. Communities living in these areas are being strongly affected by climate warming with rapid reorganizations and change in ecosystem functioning. We assess the megabenthic species composition and functional character in a transition zone around Svalbard. The relationships between environment, taxonomic composition and functional traits are investigated and discussed regarding the potential impacts of climate warming. The biomass data from 293 taxa, coded with 6 functional traits (29 modalities), from 144 trawl stations, were analyzed by multivariate statistics based on taxonomy, RLQ- and fourth corner analysis, based on environment and traits. We find that boundaries between water masses and depths are associated gradual taxonomic and sharp functional transitions. We document a biogeographic transition zone on the slope northeast of Svalbard where surface deposit feeding crustacean associations meet crawling Arctic echinoderm predators. Further we show a sharp transition at 500 m depth along the shelf of Svalbard where boreal filtrating deep-sea sponges meet a unique upraised large-bodied assemblage of bathyal species on the Yermak Plateau. Global warming will likely cause rapid taxonomic and functional shifts in these transition areas, with filtrating sponges and deposit feeding crustaceans possibly expanding into Arctic communities while large, upright, predators further down the slope. There is a need for both monitoring of the transition areas, and for protecting the most vulnerable deep and arctic fauna on the Yermak Plateau.

1. Introduction

The biogeographic transition from boreal to Arctic marine communities entails a strong species turnover documented across many phylogenetic groups (Zakharov et al., 2020a, Fraïner et al., 2021; Dalpadado et al., 2020; Albouy et al., 2020; Ramírez et al., 2017). The sharp biogeographic shift should translate in extensive functional turnover due to adaptations to the Arctic environment, as observed in demersal fish (Fraïner et al., 2017). Characterization of functional biogeography in high latitude transition zones provides important insights on biodiversity and ecosystem functioning in areas that are being strongly affected by climate warming (Violle et al., 2014). Due to rapid warming, Arctic marine ecosystems adjacent to biogeographic transition zones are presently experiencing borealization driven by poleward distributional shifts (Fossheim et al., 2015). The Barents Sea ecosystem is exposed to one of the highest rates of warming worldwide, resulting in an ‘Atlantification’ of the Arctic region of the Barents Sea (Árthun et al., 2012, Stern and Laidre, 2016; Berge et al., 2015; Fossheim et al., 2015; Misund et al., 2016, Lind et al., 2018, Barton et al., 2018, Asbjørnsen et al., 2020, Ingvaldsen et al., 2021). Over the last 4 decades, the temperature has increased by 1–1.5 °C (Lind et al., 2018), the ice-cover has decreased by 27% (Onarheim et al., 2018), and the Atlantic Water area, associated

with northward shifts in the Polar Front, has increased substantially (Oziel et al., 2016). The northern Barents Sea is experiencing the strongest declines in winter sea ice concentration and most rapid surface warming of the entire Arctic (Lind et al., 2018).

As temperature increase, many boreal marine species are either redistributing into the northern areas (Fossheim et al., 2015; Fraïner et al., 2017) or extending their distribution in the whole Barents Sea (Jørgensen et al., 2020). The ongoing rapid borealization might have profound consequences for the structure and functioning of the Barents Sea ecosystem (Fossheim et al., 2015), and the species that are most successful in entering the Arctic are species that feed on a large array of preys, i.e. generalist species (Fraïner et al., 2017; Kortsch et al., 2015; Pecuchet et al., 2020). An increase of generalist species abundance, and the concurrent decline of specialist species have been observed in many ecosystems, and can result in large-scale homogenization of the communities (Clavel et al., 2011; Ellingsen et al., 2020; Fraïner et al., 2017; McKinney and Lockwood, 1999). This functional homogenization might impact ecosystem functioning (Tilman et al., 1997), and increase ecosystem vulnerability to further environmental disturbance (Olden et al., 2004). As species from different taxonomic and functional groups redistribute with varying pace and success (Lenoir et al., 2020; Poloczanska et al., 2013), ecosystems will be increasingly composed of species

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<https://doi.org/10.1016/j.pocean.2022.102792>

that did not previously co-occur, which may result in novel species interactions and configurations (Bartley et al., 2019; Kortsch et al., 2015; Pecuchet et al., 2020).

Large-scale studies (1.5 million km²) in the Barents Sea identified temperature and depth gradients to be the most important structuring factors for both fish and benthos species (Johannesen et al., 2017). Jørgensen et al., 2015 showed that the South Western region of the Barents Sea was dominated by filter-feeders (sponges) in the inflow area of warm Atlantic water while the deeper trenches had a detritivores fauna (echinoderms). In the South western and East region, predators (sea stars, anemones, and snow crabs) prevailed together with filtering species (sea cucumber and bivalves) within a mosaic of banks and slopes. Plankton-feeding brittle stars were common in the North West and North East region, but with increasing snow crab population in North East (Zakharov et al., 2020b). A boundary line between benthos communities dominated by boreal or by arctic species stretches from the northwest to the southeast across the Barents Sea. This line varies between years and localities, with the largest spatial changes (up to 200 nautical miles) in southeastern part of the Barents Sea (Zakharov et al., 2020a).

In the present study, we investigate how the megabenthic species composition and functional character (traits) varies North and East of Svalbard, from the warmer Atlantic to cold Arctic Waters masses, and from the shallow shelf to deep abyssal areas in the west. We functionally characterize the benthic invertebrate communities around Svalbard and their environmental relationships, to help evaluate the potential impacts of climate warming on these ecosystems. Specifically, we ask whether boundaries between water masses and depth habitats are associated with sharp taxonomic transitions, to what degree the different assemblages are discriminated in terms of functional traits, and what are the relationships between functional traits and environmental gradients. We discuss the implications of our findings for functional biogeography and climate change impact in zoogeographic transition areas.

2. Materials and methods

2.1. Study area

Atlantic Water (AW) dominates the south-western part of Svalbard, and at times also farther north where various branches of the AW is crossing the Plateau occur. The West Spitsbergen Current is a slope-current transporting this AW northward along west Svalbard (Fig. 1). In the northern part of the Fram Strait, the AW flows between the 1000 and 500 m depth isobaths, with velocities up to 20 cm/s (Menze et al., 2019). When encountering the Yermak Plateau, the AW current splits into three branches; a narrow and shallow branch following the 200 m depth isobath, a branch crossing the Yermak Plateau slightly further north (near approximately 80.5°N), and a third branch flowing along the western rim of the Plateau (Menze et al., 2019, Athanese et al., 2021). The Yermak is 800–900 m deep Plateau and located at the north-western corner of Svalbard. The northern and central parts of the Plateau is usually ice-covered during winter and summer, but during the last decade the winter period have been occasionally free of ice (Athanese et al., 2020). After the AW current has passed the Yermak Plateau, it continues eastwards in a narrow band along the shelf break (Aagard, 1989) north of Svalbard. Here the flow occupies a 30–40 km wide and 75–700 m deep volume flowing between the 300–1000 m depth isobaths, with a core at 800 m (Våge et al., 2016; Pérez-Hernández et al., 2017) and with maximum mean velocity of 20 cm/s (Pérez-Hernández et al., 2019).

The circulation on the shelf is less known, but the region is influenced by the Svalbard Coastal Current transporting colder and fresher waters, exchange with the fjords, freshwater runoff from glaciers and seasonal freezing and melting of sea ice. In addition, Atlantic Water is brought onto the shelf by e.g. episodes of wind driven upwelling (Cottier et al., 2007; Goszczko et al., 2018), and by the general circulation in the trenches such as the Hinlopen trench (Menze et al., 2020), farther east in the trench northwest of Kvitøya (Pérez-Hernández et al., 2017) and farther south in the Isfjorden (Nilsen et al., 2016).

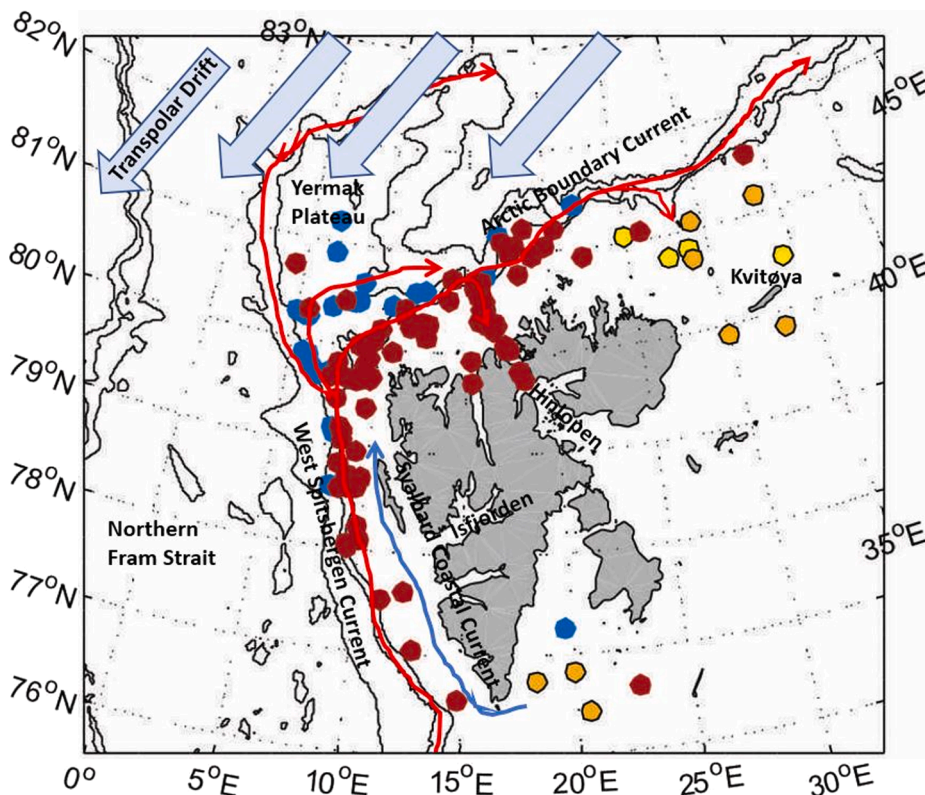


Fig. 1. The general water flow pattern west and north of Svalbard (arrows) and station network 2014–2019 categorized by the water mass present near the seabed (colored circles). Red arrows denote flow of warm Atlantic Water (in the West Spitsbergen Current), the thin blue arrow illustrate the Svalbard Coastal Current, and the thick light-blue arrows denote flow of sea ice and Polar Surface Water. The red circles define warm ($T > 0\text{ }^{\circ}\text{C}$) and salty Atlantic Water, while the blue circles cold ($T < 0\text{ }^{\circ}\text{C}$) and salty Arctic Intermediate Water. The orange and yellow circles define fresh Polar Surface Waters, and where orange have temperatures above $0\text{ }^{\circ}\text{C}$ (PSWw) and yellow below $0\text{ }^{\circ}\text{C}$ (PSW). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The along-slope flow of AW, which dominates the western and northern slope regions, is strongest in autumn and weaker in spring and early summer (Beszczynska-Möller et al., 2012; Ivanov et al., 2009; Lundesgaard et al., 2021). This causes the flow to be warmest in autumn and early winter (September–January), and with the largest vertical extent of the AW layer north of Svalbard (Renner et al., 2018). Both temperature and salinity decrease during late winter and remain low during spring and early summer. The ocean temperature on the shelf break and shelf are affected by the same seasonality, but local surface processes have more influence there complicating the pattern (Lundesgaard et al., 2021). The flow of AW across the Yermak Plateau also seems to be stronger in winter than summer (Koenig et al., 2017).

A regulation to protect vulnerable marine ecosystems (updated by Norway in 2019) banned fishery with bottom trawl below 1000 m west of Svalbard and 800 m north of Svalbard (Jørgensen et al., 2020). The regulation also tentatively closed (or protected for future) shallower areas on the shelf north and east of Svalbard. Only some regions west, north, and east of Svalbard are open for fisheries in the ice-free month of the year and only when bycatch are not considered a threat (<https://www.fiskeridir.no/Yrkesfiske/Regelverk-og-reguleringer/Fiskerimeldinger>). Bottom trawling is therefore not considered an impact factor for this study.

2.2. Surveys

2.2.1. Temperature, salinity and water masses

Temperature and salinity were measured with a Seabird CTD at all stations, including the trawl stations, each year, at the deepest sample which were 5 m above the seabed. Our characterization of the observed water masses was slightly modified after Rudels et al., (2005) and Pérez-Hernández et al., (2017) as:

- A warm and salty Atlantic Water (AW) defined by $T \geq 0^\circ\text{C}$, $S \geq 34.9$ psu, but without sigma limitations as described in Rudels et al. (2005) and Pérez-Hernández et al. (2017) on the AW because this waters currently have so high temperatures that it will be to light to fall into the AW category using the sigma characteristics of the former two studies.
- The cold and relatively salty Arctic Intermediate Water (AIW) as defined by temperature and sigma limitations ($27.97 < \sigma$, $T < 0^\circ\text{C}$). This water mass is found immediately below the AW layer in our study region.
- The fresh Polar Surface Water (PSW, $\sigma \leq 27.97 \text{ kg/m}^3$, $T \leq 0^\circ\text{C}$) that originates in the Arctic Basin as a mixture of melt/freeze water, AW, precipitation, and river runoff.
- A warmer variety of this mixture ($T > 0^\circ\text{C}$, $S < 34.9$ psu) called warm “Polar Surface Water” (PSWw) which are influenced by the warm AW and solar heating.

2.2.2. Biological sampling

The invertebrate fauna (megabenthos) was collected by 144 semi-quantitative trawl hauls during 2014–2019, with a Campelen-1800 bottom trawl (Engås and Ona, 1990) rigged with rockhopper ground gear, at depths from 125 to 1026 m. In 2016 additional floats were attached to the trawl, to avoid damage when trawling on rough ground. The hauls were standardized to a fixed sampling effort of one nautical mile. The horizontal opening was 17 m, and the vertical opening was 4 m. The mesh size was 80 mm (stretched) in the front and 24 mm in the cod end, allowing the capture and retention of small-sized fish and the largest benthos (benthic megafauna) from the seabed. In addition, the trawl may also be contaminated by organisms entering the trawl when it is lowered or heaved.

The catch from the 144 bottom trawls was identified to lowest possible taxonomic level and resulted in 293 megabenthic taxa, of which 135 were classified at the species level, 79 at family level, and the rest at lower taxonomic resolution.

Wet-weight biomass was recorded with electronic scales (Marel series1100) in the ship laboratories, and the numbers of individuals were noted for each taxon. For colonial organisms (sponges, colonial ascidians, bryozoans, hydrozoans), only weights were recorded. The biomass determination included all fragments.

After removing pelagic, adult taxa, all individuals were included in subsequent data analysis whether identified to species or to a higher taxonomic level. Only animal fragments with the head-part intact were counted, but as colonial species could not be counted.

2.3. Analyses

2.3.1. The taxonomic faunal analyses

To classify the benthic communities based on their taxonomic composition, we performed a hierarchical cluster analysis on \log_{10} transformed biomass data of benthic taxa, using Bray-Curtis dissimilarity with complete linkage method (max linkage method). The Bray-Curtis dissimilarity is commonly used in community ecology, including benthic studies, as it provides an intuitive measure of structural dissimilarity between samples expressed in percentage (Legendre and Legendre, 2012). Use of complete linkage ensured the identification of clearly distinct clusters in terms of community structure (Greenacre and Primicerio, 2013). Visual inspection of the dendrogram generated by hierarchical clustering allowed to specify a suitable number of sharply distinct faunal groups (clusters), while retaining a number of stations (a minimum of 10) per cluster that guaranteed sufficient spatial coverage. Each cluster contained several hundred species/taxa, many of which were rare. To avoid describing fauna based on rare species, only species/taxa recorded at all or most stations within a station cluster were used in the taxonomic characterization together with dominant taxa with the highest biomass. The clustering was performed using software PCORD 6.0 (MjM Software, Gleneden Beach, Oregon, USA, Peck, 2010).

The classification of benthic groups was complemented with an ordination analysis of community structure using non-metric multidimensional scaling (NMDS, Cox and Cox, 2001). To harmonize with the hierarchical clustering, the NMDS was based on the same Bray-Curtis dissimilarity matrix, and the clusters of stations were depicted in the NMDS maps to relate the clustering and ordination results (Legendre and Legendre, 2012). In order to represent the environmental gradients that separate faunal clusters in the ordination maps, the environmental variables “depth”, “temperature”, “salinity” and “days of ice-cover” were projected on the ordination map by regressing these variables against the NMDS axes (Greenacre 2010). Five hundred iterations with real data were made, with 10 iterations used to evaluate model stability based on a stability criterion of 10^{-7} . An initial 6-dimensional NMDS was performed to search for an optimal number of axes that best represented the variation in the data set. Following a scree plot inspection, it was determined that a three-dimensional NMDS ordination with final instability of 10⁻⁷ and stress value (goodness of fit) of 11.24 was adequate to account for most of the observed variability. The NMDS were based on Bray Curtis distance and were performed using software PCORD 6.0 (MjM Software, Gleneden Beach, Oregon, USA, Peck 2010).

2.3.2. Trait-environment relationships

We collected information on six traits to broadly characterize the ecological niche and feeding strategies of the sampled benthic species: body size, body-form, skeleton, movement, speed and feeding habit (Table 1). These traits are relevant for ecosystem functions such as production and nutrient cycling (Törnroos and Bonsdorff, 2012). The six traits were further separated into multiple modalities which were fuzzy coded based on how much affinities a species has for each modality: (0) no affinity, (1) low affinity, (2) high affinity, and (3) total and exclusive affinity (Chevenet et al., 1994). Then, we transformed the fuzzy coded modalities into proportions so that their sum equaled one for each trait and species (i.e., for each species we divided each modality value by the sum of its trait modalities). The trait values were obtained from the literature and from

Table 1
The 6 adult traits and 29 modalities and the definitions (Degen and Faulwetter 2019).

Morphological traits to survive and be resistant	Size	Small (S1)	(S1)	<10 mm
		Small-medium	(S2)	10–50 mm
		Medium	(S3)	50–100 mm
		Medium-large	(S4)	100–300 mm
		Large	(S5)	>300 mm
	Form	Globulose	(BF1)	Round or oval (e.g. sea urchin, sponge, some bivalves)
		Vermiform, elongate	(BF2)	Worm-like or thin, elongate body form
		Dorso-ventral compressed	(BF3)	Species that are flat, or encrusting (e.g. starfish, sponge)
		Laterally compressed	(BF4)	Thin (e.g. isopods, amphipods, some bivalves)
		Upright	(BF5)	E.g. coral, basket star, sponge
	Skeleton	Calcareous	(SK1)	Skeleton material aragonite or calcite, e.g. bivalves
		Siliceous	(SK2)	Skeleton material silicate, e.g. siliceous sponges
		Chitinous	(SK3)	Skeleton material chitin, e.g. arthropods
		Cuticle	(SK4)	No skeleton but a protective structure like a cuticle, e.g. sea-squirts
		None	(SK5)	No form of protective structure, e.g. sea slugs
Behavioral traits for adapting to environment	Movement	Sessile/none	(MV1)	No movement as adult (sponge, coral)
		Burrower	(MV2)	Movement in the sediment (e.g. annelids, echinoderms, crustaceans, bivalves); including tube dwellers.
		Crawler	(MV3)	An organism that moves along on the substratum via movements of its legs, appendages or muscles (e.g. crab, snail)
		Swimmer (facultative)	(MV4)	Movement above the sediment (e.g. Amphipoda)
	Speed	None	(MO1)	No movement as adult (sponge, coral)
		Low	(MO2)	Slow movement (e.g. anemones, some polychaetes, burrowing organisms)
		Medium	(MO3)	Medium movement (e.g. starfish, brittle stars)
		High	(MO4)	High movement, swimmer or fast crawler (e.g. crabs, shrimps)
	Feeding	Surface deposit feeder	(FH1)	Active removal of detrital material from the sediment surface. Includes species which graze

Table 1 (continued)

		Subsurface deposit feeder	(FH2)	or scrape algal matter from surfaces. Removal of detrital material from within the sediment matrix (e.g. Echinocardium)
		Filter/suspension feeder	(FH3)	Sponge, coral, hydrozoa, bivalves
		Opportunist/scavenger	(FH4)	An organism that can use different types of food sources/an organism that feeds on dead organic material (e.g. crabs, whelks)
		Predator	(FH5)	An organism that feeds by preying on other organisms (e.g. starfish).
		Parasite/commensal/symbiotic	(FH6)	An organism that lives in or on another living organism (the host), from which it obtains food and other requirements; or an organism containing symbionts.

benthic trait databases such as SeaLifeBase (www.sealifebase.ca/), LifeWatch (www.lifewatch.be/en/marine-species-traits), MARLIN (MarLIN, 2006), The Arctic Traits Database (Degen and Faulwetter, 2019), and corresponds to average trait value for an adult individual of each species, i. e., each species were assigned one value per trait and thus intra-species variation was not considered.

We investigated potential relationships between the trait composition of the benthic communities and the environmental variables by RLQ analysis and fourth corner analysis (Dray et al., 2014). These methods assess the trait-environment relationship by analyzing three Tables: the environmental values per station (R), the species composition per station (L) and the trait values per species (Q). RLQ analysis estimates the relationships among sites, species, environmental variables, and traits using simultaneous ordination (Dolédec et al., 1996). The three Tables (R, L, Q) were transformed before performing the RLQ analysis, using a principal component analysis for the environment (R), a correspondence analysis for the species community composition (L) and a fuzzy principal component analysis for the species' trait matrix (Q, Chevenet et al., 1994). We tested the significance of the RLQ axis using 999 random permutations. Fourth corner analysis estimates the Pearson's correlation coefficient between each trait modality and each environmental variable (Dray and Legendre, 2008). We corrected p-values for multiple comparison using false discovery rates for the fourth corner analysis. As for the taxonomic analyses, species biomass was log-transformed before doing these trait-based analyses. Due to skewness, the environmental variables depth, current and number of ice-covered days were log-transformed before analysis. We used the R package "ade4" for these analyses (Dray and Dufour, 2007).

3. Results

3.1. Horizontal distribution of water masses

Warm and salt, relatively fast moving, Atlantic Water dominates in the near bottom layers along the slope (Fig. 1). This water mass also

dominates on the shelf west and north of Svalbard to about 25°E, while the fresher Polar Surface Waters of Arctic origin dominate to the east of Nordaustlandet (northeast of Svalbard). Most of the Polar Surface Water in the region has temperatures above 0 °C, with some stations being colder than 0 °C. The Yermak Plateau is dominated by the cold Arctic Intermediate Water, mostly located below the Atlantic Water. However, some stations at the Yermak Plateau are also dominated by Atlantic Water, probably due to the crossing AW flow. South of Svalbard (in the Storfjorden trench), both Polar Surface Water, Atlantic Water and Arctic Intermediate Water occurred.

3.2. The clustering of stations based on taxonomy

Based on 287 identified taxa (119 to species level) the stations were clustered together based on their species composition, and the six clusters selected by visual inspection of the dendrogram contained between 10 and 55 stations (Supplementary material Figure S1 and Table S1). Within each cluster, the sampling years 2014 (28 stations), 2015 (26 stations), 2016 (14 stations), 2017 (27 stations), 2018 (23 stations) and 2019 (27 stations) were mixed. This means that interannual variation does not structure the observed species composition and must be relatively small, the different sampling years were therefore pooled. When regressing the environmental variables against the nonmetric multidimensional scaling (NMDS) axes, “depth” and “temperature” showed the strongest association with the first two ordination axes (Supplementary material Figures S2, S3).

Two station clusters included the deepest stations in this study, extending far north, and mainly on the Yermak Plateau (clusters 13-white triangles and cluster 24-yellow circles Table 2) in waters mainly characterized as relatively low-saline, cold Arctic Intermediate Waters (AIW). The stations within cluster 24 had a mean temperature of -0.4 °C (range, -0.8 °C to 0.3 °C) and salinity of 34.93 (range, 34.92 to 34.95) and the longest annual sea ice cover with an average of 215 days (Table 2).

Two clusters were distributed along the continental slope (1-blue circles and 17-green boxes) and were almost entirely confined to saline Atlantic Water, with only very few stations in the colder Arctic Intermediate Water (Table 2). The temperature ranged from -0.3 °C to 4.8 °C with an average of 3.0 °C and the salinity ranges from 34.42 to 35.12.

Two clusters were widely distributed on the shelf all around Svalbard (2-red and 10-orange) in both AIW (only one station), AW as well as in cold low-saline Polar Surface Water (PSW, Table 2) and on the shallowest stations.

3.3. Biological characteristics of the station clusters

The species richness, within a cluster, varied from 95 taxa farthest to the north on the deep Arctic Yermak plateau (cluster 24, mean depth 916 m) to 212 taxa on the relatively shallow shelf around Svalbard (cluster 2, mean depth 365 m) (Table 2). The highest recorded mean biomass was found in cluster 1 located along the slope. The lowest mean biomass was in cluster 24 on the deep Arctic Yermak Plateau. Three of the six station clusters had biomass-dominant species/taxa presented at each of the stations within the cluster (see in bold in Table 2), while other biomass dominant species (mean value across all stations within the cluster) may be widely distributed within the cluster, but not present at all stations.

3.3.1. The faunal associations on the slope

Geodia sponge aggregations (station cluster 1) was located deep (mean depth 432 m, Table 2) on the slope within fast-moving, warm Atlantic Waters (Fig. 2). This cluster made up the largest mean biomass with 94% made up by sponges, and the largest mean body-weight. The large-bodied sponge *Geodia* sp made up to 798 kg/nm taken by the trawl. Together with other sponges the Porifera made up 94% of the total biomass in this station cluster. Other, but less dominant, species

were the shrimp *Pandalus borealis* and the sea star *Henricia* sp. presented at 16 out of 17 stations. The brittle stars *Ophiopholis aculeata* and *Ophiura sarsii*, the sea star *Crossaster papposus*, the sea urchin *Strongylocentrotus* sp, the Cauliflower corals (Nephtheidae), and the lamp shell *Terebratulina retusa* was present at 15 of the stations.

The widely distributed heterogenous fauna (stations cluster 17) was recorded on the shelf west and north of Svalbard from 120 m depth and down to 1031 m depth. Arctic Waters was only recorded at the deepest station, while all other stations varied from 1.04 to 4.83°C (Fig. 2). The biomass of this cluster was distributed across several different phyla (Table 2), resulting in <10% fauna similarity among the two most different stations. A total of 146 species were recorded in this cluster and no species were present at all stations. A variety of undefined sponges (NB: not *Geodia* species) and the widely distributed crevice brittle star, *Ophiopholis aculeata*, were recorded on 14 out of 16 stations, while the sea urchin *Strongylocentrotus* sp. and the sea spider *Nymphon hirtipes/spinosum* were recorded on 12 stations. *Chlamys islandica* and *Ophiura sarsii* were recorded at 11 stations.

3.3.2. The arctic fauna associations

The cold-water medusa-head *Gorgonocephalus* sp. (station cluster 13), were recorded on all stations within this cluster, and were also among the top biomass (Table 2) together with the sponge *Haliclona* sp and the sea star *Bathybiaster vexillifer*. This cluster, at 155–1086 m depth (mean depth 791 m), was located on the Arctic Yermak Plateau but also on the slope north-west of Svalbard, in the Storfjord southeast of Svalbard and on the shelf north-east of Svalbard across a wide temperature range (Fig. 2). The cluster included 184 species. The cauliflower corals (Nephtheidae) and the amphipod *Anonyx* sp dominated 12 out of the 15 stations while sponges, the sea spiders *Boreonymphon* sp/*Colosendeis* sp and the sea star *Henricia* sp dominated 11 stations.

The arctic bathyal shrimp *Hymenodora glacialis* (station cluster 24), were recorded on all stations in the cold Arctic Intermediate Water furthest to the north on the deep Yermak plateau (736–1111 m) (Fig. 2, Table 2). This station cluster was represented by 95 species and dominated by crustaceans. At 7 to 9 of the 10 stations were the shrimp *H. glacialis* recorded together with the arctic bathyal shrimp *Bythocaris* sp, and amphipods such as the large bathyal arctic *Eurythenes gryllus*, the ice-associated (sympagic) *Eusirus holmi* and *Anonyx* sp. Here the sea pen *Umbellula encrinus* and the cephalopod *Cirroteuthis muelleri* made up the large biomasses (up to 5 kg/nm) but were only recorded at 6 and 4 out of the 10 stations respectively.

3.3.3. The stations on the shelf

Station **cluster 2 and 10**, distributed all around Svalbard, differ from the four other station clusters by having substantially wider temperature and salinity ranges (Fig. 2).

The shrimp *Pandalus borealis* dominated association (station cluster 2) was widely distributed around Svalbard, *except* on the Arctic Yermak Plateau (Fig. 2). The *P. borealis* was present at all stations (Table 2) and the largest catches in number of individuals was within this station cluster and due to this shrimp. Most catches were <5 kg/nm. But the largest catches were from the Hinlopen strait (39–61 kg/nm) and inside the Barents Sea east of Svalbard (175 kg/nm). Nearly all stations included the sea star *Ctenodiscus crispatus* and the brittle star *Ophiura sarsii* (45 and 49 out of 55 stations respectively). Other less frequent distributed taxa included the crab *Hyas* sp, sponges.

The echinoderm dominated faunal association (station cluster 10) was widely distributed around Svalbard from the warm Atlantic Waters in the south and northward into the Arctic Waters of the Yermak Plateau and north east of Svalbard (Fig. 2). This cluster was the most species-rich (212 taxa), though the stations shared > 13,40 % of the fauna similarity. No species was recorded at all stations, but the sea anemone *Hormathia* spp were found at 21 out of the 24 stations. The crevice brittle star *Ophiopholis aculeata* and the polychaeta *Polynoidae* sp. were recorded at 20 stations. The crangonid shrimp *Sabinea*

Table 2

Summary of the average taxonomic and environmental values for each cluster. The cluster number, and number of stations within the cluster, and the area name. The most biomass dominant taxa/species (kg/nm) and with highest occurrence (%) across the station cluster. The faunal similarity (see material and method for explanation). Total taxa richness within the cluster and the mean taxa number per trawl. The mean trawl biomass (kg.nm) and body weight (kg). The mean depth (m) with minimum and maximum depths. The mean temperature (°C) and numbers of ice days per year. The mean salinity (‰). A general description of the fauna within the station cluster. The water characteristic across station: Atlantic Water (AW), Arctic Intermediate Water (AIW), fresh Polar Surface Waters above 0 °C (PSWw) and below 0 °C temperature (PSW).

Cluster (stations) Area	The most biomass dominant taxa/species (kg/nm) and with highest occurrence (%)	Fauna-sim %	Taxa per cluster (mean per trawl)	Mean kg/nm (body-weight)	Depth mean m (min–max)	Mean Temp °C (ice days)	Mean Salt ‰	General description of biomass among phyla	Water characteristic (number of stations)
1 (17) Slope	<i>Geodia</i> (117,0 kg; 100%) <i>Porifera</i> (18,9 kg; 100%) <i>Stryphnus</i> (5,9kg/47%) <i>Pandalus borealis</i> (5,2 kg; 94%) <i>Polymastiidae</i> (0,24; 82%) <i>Ophiopholis aculeata</i> (0,1 kg; 82%) <i>Nephtidae</i> (0,1 kg; 82%) <i>Strongylocentrotus</i> (0,06 kg; 82%) <i>Crossaster papposus</i> (0,04 kg; 82%) <i>Henricia</i> (0,03 kg; 94%) <i>Terebratulina retusa</i> (0,02 kg; 88%)	29,6	194 (49,9)	145,5 (6,63)	432 (169–1020)	3,01 (51)	35,03	94% Porifera , 3,7% Crustacea, The remaining 2,1% biomass distributed among 13 phyla.	AW (17)
2 (55) Shelf Hinlopen	<i>Pandalus borealis</i> (22,4kg; 100%) <i>Hyas</i> sp.(2,1kg; 43%) <i>Ctenodiscus crispatus</i> (1,4kg; 84%) <i>Ophiura sarsi</i> (0,2kg; 89%)	35,9	209 (34)	28,44 (0,68)	365 (132–566)	2,74 (85)	34,97	86,8% Crustacean , 8,1 % Echinodermata, 5% distributed on 12 phyla	AW (47) PWWw (4) PSW (1)
17 (16) Slope	<i>Forcepia</i> sp. (0,16 kg; 12%) <i>Pasiphaera</i> sp. (0,16 kg; 19%) <i>Porifera</i> (0,14 kg; 865%) <i>Chlamys islandica</i> (0,12 kg; 69%) <i>Ophiopholis aculeata</i> (0,02 kg; 88%) <i>Strongylocentrotus</i> (0,01 kg; 75%)	9,6	146 (31,1)	1,06 (0,30)	344 (112–1031)	3,06 (66)	35,00	39,1% Crustacea , 32,2% Porifera , 14,3 Mollusca , 7,8% Mollusca. The remaining 6,5% biomass distributed among 8 phyla.	AW (15)AIW (1)
10 (24) Shelf	<i>Ctenodiscus crispatus</i> (0,8kg; 75%) <i>Strongylocentrotus</i> sp. (0,7kg; 63%) <i>Molpadia</i> sp. (0,5kg; 33%) <i>Urasterias lincki</i> (0,4kg; 33%) <i>Sabinea septemcarinata</i> (0,3kg; 79%) <i>Hormathia</i> sp (0,1kg; 88%) <i>Ophiopholis aculeata</i> (0,03 kg; 83%) <i>Nephtidae</i> (0,01 kg; 79%) <i>Polynoidae</i> (0,01 kg; 83%)	13,4	212 (43)	5,90 (0,61)	221 (83–985)	1,94 (1 34)	34,88	58,6% echinoderms , 16,9% Crustacea , 10,3% Porifera , 5,1% Cnidaria. The remaining 9% distributed among 10 phyla.	AIW (2)AW (15)PSW (3)PSWw (4)
13 (18) Slope Shelf	<i>Gorgonocephalus</i> sp. (8,4kg; 100%) <i>Bathybiaster vexillifer</i> (0,7kg; 33%) <i>Haliclona</i> sp. (0,6kg; 28%) <i>Pandalus borealis</i> (0,5kg; 55%) <i>Porifera</i> (0,4kg; 78%) <i>Nephtidae</i> (0,03 kg; 83%) <i>Anonyx</i> (0,02 kg; 83%)	27,9	184 (42)	13,63 (1,21)	791 (155–1086)	–0,21 (82)	34,93	73,2% echinoderms , 9,9% Porifera, 9,1% Crustacea. The remaining 7,8% distributed among 12 phyla.	AIW (14)AW (3)PSWw (1)

(continued on next page)

Table 2 (continued)

Cluster (stations) Area	The most biomass dominant taxa/species (kg/nm) and with highest occurrence (%)	Fauna-sim %	Taxa per cluster (mean per trawl)	Mean kg/nm (body-weight)	Depth mean m (min-max)	Mean Temp °C (ice days)	Mean Salt ‰	General description of biomass among phyla	Water characteristic (number of stations)
	<i>Boreonymphon</i> sp (0,01 kg; 78%) <i>Henricia</i> (0,01; 78%)								
24 (10) Yermak	<i>Umbellula encrinus</i> , (1,1kg; 60%) <i>Hymenodora gracilis</i> (0,4kg; 100%) <i>Cirroteutis</i> sp. (0,1kg; 30%) Axinellidae, (0,1kg; 10%) <i>Bythocaris</i> sp (0,1kg; 70%) <i>Eurythenes gryllus</i> (0,1kg; 80%) <i>Eusirus holmi</i> (0,01 kg; 80%) <i>Anonyx</i> sp (0,01 kg; 90%)	19,0	95 (24,4)	2,12 (0,40)	916 (729–1111)	−0,41 (215)	34,92	47,6% Cnidaria, 28,7% Crustacea, 9,1% Echinodermata, 7,1% Mollusca, 5,7% Porifera. The remaining 1,8% distributed among 6 phyla.	AIW (9)AW (1)

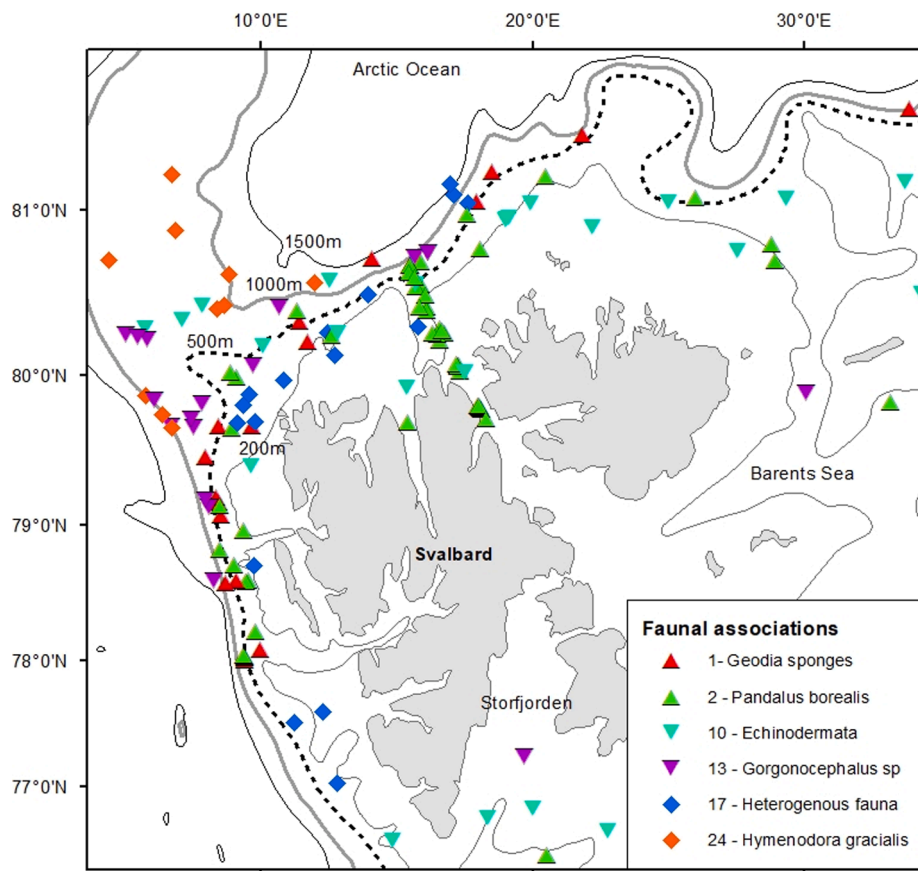


Fig. 2. The biogeographic distribution of the six station clusters based on taxonomic similarity for the Atlantic clusters “1”, “13”, “17” and “24”, and the Arctic clusters “2” and “10”. The 500 m depth isobath (broken black line) is shown together with the isolines of 200, 1000 and 1500 m depths (black and gray lines).

septemcarinata and the cauliflower corals (Nephtheidae) was recorded at 19 stations. The most biomass dominant were echinoderms such as sea cucumber (*Molpadia borealis*), sea urchin (*Strongylocentrotus* sp), sea stars (*Urasterias linkii* and *Ctenodiscus crispatus*) and the polymastiidae sponge *Polymastia hemisphaerica*.

3.4. Trait composition and environmental variables

The first two axes of the RLQ analyses explained 98.7% of the projected co-inertia, with the first axis explaining 86.4% and the second axis

12.3%. The analysis revealed that a water mass with high number of ice-days, low salinity and low temperature (Fig. 3 right side of the upper right panel) represented the trait modalities “calcareous skeleton (SK1), flat (BF3), medium body size (S3), crawlers (MV3), with a medium movement (M03) (Fig. 3 right side of the upper left panel). The species belonged to echinoderms and included the sea urchin *Strongylocentrotus* spp., several sea star species (e.g. *Bathybiaster vexillifer*, *Leptasterias muelleri*, *Ceramaster* spp., *Lophaster furcifer*, *Ctenodiscus crispatus*, *Urasterias linkii*) and the brittle star *Ophiura sarsii* (Fig. 3 right side of the lower panel). A fourth corner analyses revealed a weak association

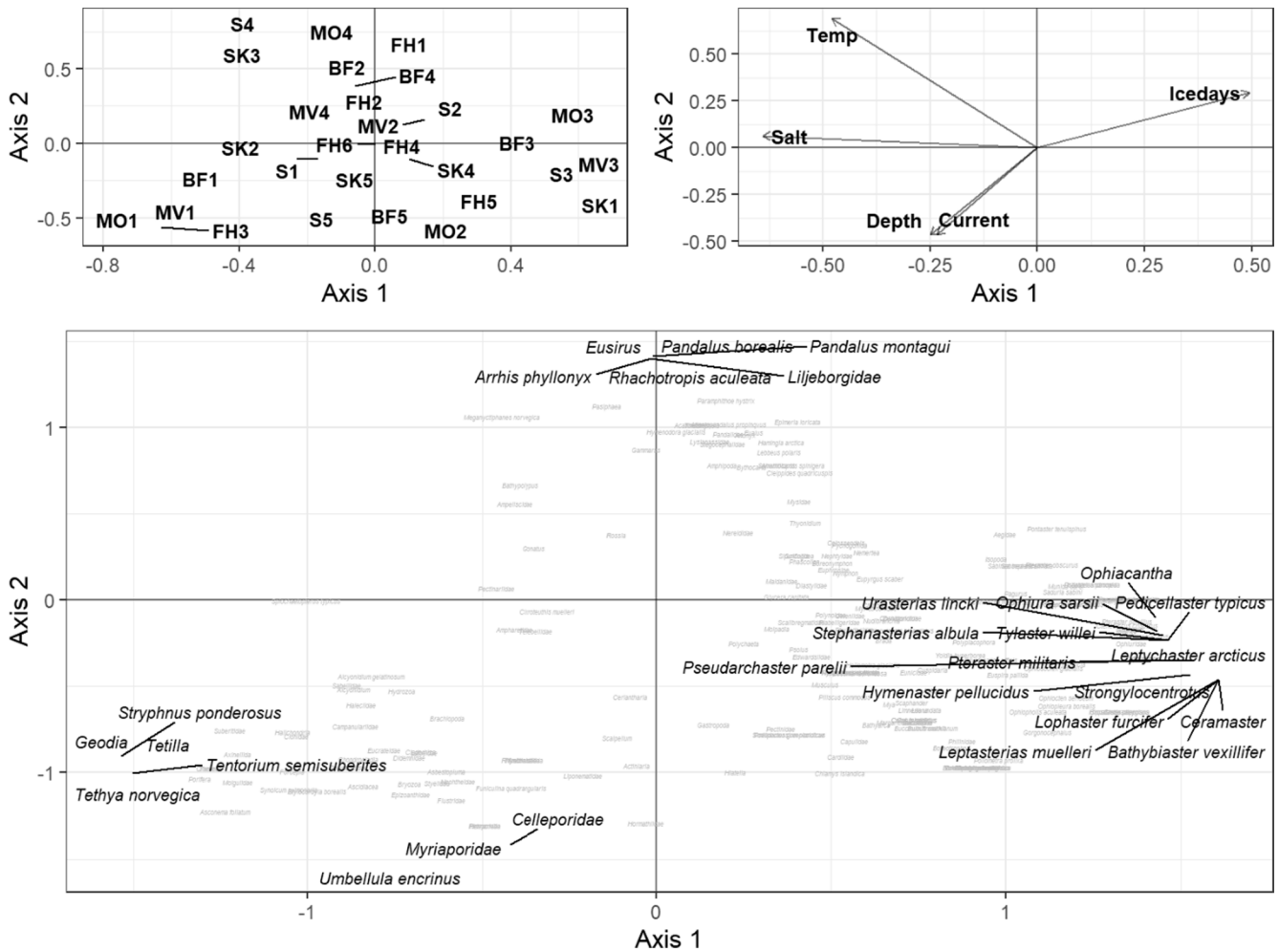


Fig. 3. Results of the RLQ analysis. Loadings along the first and second RLQ axis for: (top left) traits, (top right) environmental variables and (bottom) species biomass. The first and second RLQ axis represent 86.4% and 12.3% of the projected co-inertia, respectively. Due to readability, we highlighted the species with a high loading along the first or second axis (> -1.4 and $> +1.4$).

between “many ice days and calcareous skeleton/crawling” and “low salinity and calcareous skeleton/crawling with medium movement” (Supplementary material Figure S3).

The relatively deep (around 500 m), current-rich seabed with high salinity, high temperature (Fig. 3 bottom left side of upper right panel) represented the trait modalities “sessile (MO1, MV1), siliceous skeleton (SK2), globulose (BF1), and filter/suspension feeder (FH3)” (Fig. 3 right side of upper left panel). The species belong to a variety of sponges including *Geodia* spp., *Tentorium semisuberites*, *Tethya norvegica*, and *Stryphnus ponderosus* (Fig. 3 left side of lower panel) and represented the species identified by the cluster analyses (Table 2). The “fourth corner analyses” revealed a significant association between “high current and filter/suspension feeders and “high salinity/few ice days and siliceous skeleton/sessile/non-moving/globules/filter/suspension feeders” (Supplementary material Figure S3). The stations characterized by this species assemblages, trait and environment were located in the Atlantic Water along the slope west and north of Svalbard (dark blue circles and red circles in Fig. 4a).

The shallow areas (around 200 m) with highest temperatures, high salinity, and low current (Fig. 3 upper part of the upper right panel) represented the trait modalities “high movement (MO4), surface deposit-feeders (FH1), and vermiform (BF2) or laterally compressed (BF4) body shape, medium large (S4) and chitinous (SK3) (Fig. 3 upper part of the upper left panel). The species belong to the amphipod species (*Arrhis phyllonyx*, *Rhachotropis aculeata*, *Eusirus* spp. and *Liljeborgidae*),

and the shrimps *Pandalus borealis* and *P. montagui*. The stations characterized with this species assemblages, trait and environment were located on the shallow shelf, west and north of Svalbard (Fig. 4b grey circles).

The offshore (Fig. 4b black circles) deepest areas (below 500 m) with high water-current and the lowest temperatures (Fig. 3 lower part of the upper right panel) represented the trait modalities “large (S5), upright (BF5)” and predator (FH5) (Fig. 3 lower part of the upper left panel). The species included the sea pen *Umbellula encrinus*, and the bryozoan taxa *Myriaporidea* and *Celleporidae*. A fourth corner analyses revealed a significant association between “deeper depths and large body-size”.

3.4.1. Combining biogeography with morphological functions

The clustering (chapters 3.2 and 3.3.) biogeographic analyses is based on the taxonomic similarities among stations, while the RLQ (chapter 3.4) is a morphological analysis based on how the environment filters trait abundances. The RLQ method picks stations from several taxonomic station clusters (Supplementary Table S2) as long as a station, based on environment, are dominated by a certain trait-based phyla.

This results in the RLQ lumping (Fig. 3 lower left) the current-rich warm Atlantic Water stations (red circles in Fig. 4a) and dominated by sessile, filtering Porifera (cluster 1) and Heterogenous fauna (cluster 17) from the deeper slope, while fast moving, detritivore shrimps (cluster 2) from the shallower shelf (see appendix Table S1). The RLQ therefore links the current-rich, deep sponge species on the left side of the lower

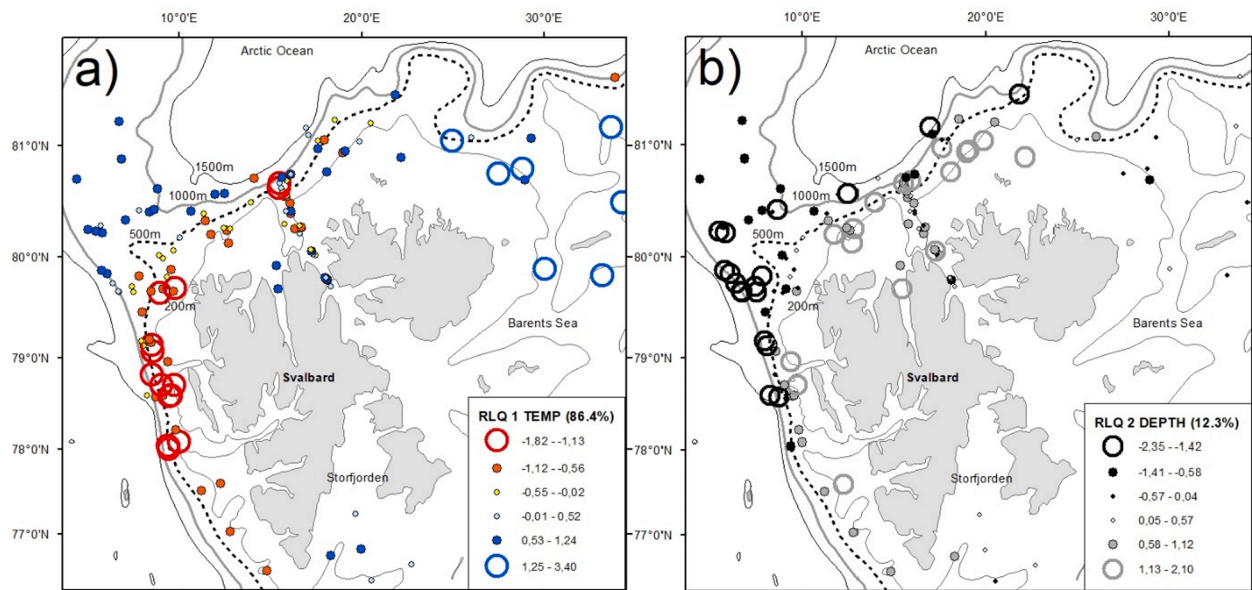


Fig. 4. a-b. Map of stations highlighting the RLQ results, a) The first axis (RLQ 1) captures a gradient from Arctic (blue) to Atlantic (red) conditions, and b) the second axis (RLQ 2) a gradient from deep cold (black, >500 m) to shallow warm water (gray, <500 m). The 500 m depth isobath (broken black line) is shown together with the isolines of 200, 1000 and 1500 m depths (black and gray lines). The stations with extreme RLQ scores along the first or second RLQ axes are shown with open circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 3 to the current-low, shallower shrimp and amphipods in the upper middle, while to a diverse fauna in other parts of the figure.

With gradually decreasing temperatures (moving from the left to the right in Fig. 3) the slow crawling, flat Echinoderma (cluster 10) get included, with *Gorgonocephalus* (cluster 13) in deeper waters and shrimps (cluster 2) from the shallower shelf. The *Hymanodora gracialis* (cluster 24) on the Yermak Plateau, iconized as large upright predator “*Umbellula encrinus*” by the RLQ, are manifested as both the shallow cold Echinoderms (right side of RLQ) and the deeper warm Porifera (left side RLQ) gradually transits into deeper Arctic waters (middle RLQ) (see Appendix Table S1).

4. Discussion

The megabenthic fauna composition of the Arctic Barents Sea shows a gradual transition from a boreal to an arctic, and from a deep to a shallow water taxonomic association, and with sharp morphologic transition zones. One transition, from Boreal to Arctic fauna, is located northeast of Svalbard, where Atlantic and Arctic water masses meet, while the other, from shallow to deep, was at the 500 m depth isobath facing the Arctic Ocean and the Greenland Sea. The Boreal assemblages along the west and northern slope and shelf of Svalbard, found in current-rich, warm Atlantic Water, where functionally characterized as sessile, slow-growing and long-lived, filter-feeding aggregations of sponges and associated species. The Arctic assemblages on the shelf northeast of Svalbard, found in low-saline, cold, Surface Polar Water with low current and extensive ice-cover, were characterized by crawling, calcareous, flat-bodied, echinoderms. The shallow, warm Atlantic shelf west and north of Svalbard, had a faunal association dominated by fast moving, surface-deposit feeding shrimps and amphipods. The deep areas below 500 m, on the remote, ice-covered, northernmost extension of the Norwegian continental shelf (the Yermak Plateau) overflowed by the cold Arctic Intermediate Water was significantly related to a peculiar and unique faunal assemblage with large-bodied, upright sea-pens.

This combination of a biogeographic mapping combined with a description of how the environment filters certain species traits (the morphological function) shows that taxonomic clustering and a RLQ analyses provides a mutual benefit.

4.1. A warm sponge transit into cold echinoderms.

This work shows that a warm water boreal sponge associations are distributed in Atlantic Water, a finding also recorded previously by Keđra et al., (2017), Davidson et al., (2019) and Knudby et al., (2013), and locally along the continental-break of the Barents Sea and the Norwegian west coast (Jørgensen et al., 2015, Jørgensen et al., 2016), where fast-moving water (Roberts et al., 2018) provides them with large amounts of sinking or advected particles to filter (Tjensvoll et al., 2013). This continental break association was clearly identified by the biogeographic- and by the morphologic analyses in this work and localized in deep Atlantic warm water west and north of Svalbard. The dominant sponges are resistant to temperature increase (Strand et al., 2017), and the ongoing Atlantification in the Barents Sea (Skagseth et al., 2020, Ingvaldsen et al., 2021) may promote an expansion of their distribution. The limited available knowledge of deep-sea sponges (Last et al., 2020) suggests that their expansion will be gradual, as they release gametes twice a year (Spetland et al., 2007) with larvae settling in the vicinity of the parental populations (Mariani et al., 2006, Knudby et al., 2013). The Boreal sponge association identified in this work had the highest species/taxa diversity per trawl haul, compared to the other five faunal associations. As the sponges expand into new areas, they promote an increase in biodiversity by facilitation, giving rise to a rich marine benthic biotope of sponge surfaces, canals and inner tissues colonized by many species (Clavico et al., 2006, Klitgaard, 1995, Mortensen and Fosså, 2006, Roberts et al., 2006), and which can serve as attractive foraging area and structural habitat for fish seeking food and shelter (Auster, 2005, Harter et al., 2009, Miller et al., 2012, Buhl-Mortensen et al., 2012; Knudby et al., 2013). Monitoring the sponges will reveal if an expansion deeper on the Yermak Plateau and into the prevailing Arctic environment is possible, and if the deep-sea sponges manage to climb the geographical barrier up upon the shallow north-eastern shelf, currently populated by Arctic fauna.

A arctic faunal association was clearly identified by the biogeographic- and by the morphological analyses in this work, on the shallower shelf south and north of Svalbard, dominated by echinoderms (sea star, brittle star, sea urchin and sea cucumber). This association has also previously shown to characterize these areas (Jørgensen et al., 2015, Piepenburg et al., 1996a,b, Piepenburg, 2000), with echinoderms often

responsible for most of the biodiversity (Gebrek et al., 2010) down to the Arctic abyssal regions (Rybakova et al., 2019). Many sea stars are keystone species capable of adapting to different environments and maintaining high species diversity, in part due to them being major predators on a diverse range of species (Paine, 1969, Menge and Sanford, 2013). *Leptychaster arcticus* is a predator on small infaunal animals (Parzanini et al., 2018), Hippasterias phrygiana fed on several species of soft coral and Ceramaster granularis fed on sponges. Predator echinoderms can adapt to different environments because they predate and scavenge on a diverse array of prey species (Paine, 1969, Menge and Sanford, 2013; Parzanini et al., 2018; Gale et al., 2013). On the other hand, are *Leptychaster arcticus* and the boreal-Arctic, eurybathic sea star *Ctenodiscus crispatus* feeding infaunally on bulk sediment and molluscs (Gale et al., 2013) and *C. crispatus* are known to prefer a stable physical environment and a rich detrital food source. The abundance of *C. crispatus* is correlated with phytoplankton production rather than temperature (Shick et al., 1981), and together with the arctic sea cucumber *Molpadia borealis*, it forms dense local populations in areas with soft, muddy sediment that is rich in organic matter (Anisimova et al., 2011), often in concordance with marginal ice zones, polynyas and gyres and influenced by water column processes controlling primary production, particle sedimentation and, hence, ultimately food supply to the benthos (Piepenburg, 2000). Climate warming will expose the Arctic to increased thermal stratification, resulting in a decrease of food-supply to the bottom (Wassman and Reigstad 2011), which may impact the distribution and frequency of detritivore echinoderms. Benthivory seems to be a successful feeding habit in the Arctic, being also common among fish (Frainer et al., 2017), and could be a characteristic feature across the entire demersal Arctic.

4.2. A shallow crustacean transit into deep crustacean-cnidarians

The biogeographic analyses identified a faunal association dominated by the shrimp *Pandalus borealis* and occasionally by crabs. This was recorded mostly on the shallow shelf flooded by shallow, warm Atlantic shelf west and north of Svalbard. Some of the northern shrimp populations may have sufficient adaptive capacity to benefit from future moderate warming (Ouellet et al., 2017), but *P. borealis* thrives under relatively stable conditions (Le Corre et al., 2020) and is vulnerable to long-term climatic changes (Koeller et al., 2009). Because this shrimp species is an important prey in the marine food web (Parsons, 2005, Kortsch et al., 2015), a reduction in the shrimp population may impact many predator species of the shelf ecosystem. It also remains to study if the shrimps expand into Arctic areas currently inhabited by the Echinodermata as waters get warmer and less ice-covered.

Numerous crustacean amphipods (*Eusirus sp.*, *Liljeborgidae Arrhis phyllonyx*, *Rhachotropis aculeata*) semi quantitatively collected by the 0.8 cm mesh-sized bottom trawl and recorded within several biogeographical areas, were weakly identified by the morphological analyses for the warm and shallow shelf. These medium large and chitinous amphipods are functionally important and can create extremely productive communities (Highsmith and Coyle, 1990). Amphipods may feed continuously, taking advantage of a variety of food sources that are available year-round in shallow waters (Legeżyńska et al., 2012), establishing important trophic links with primary and secondary producers, as well as being a main food source for fish, birds and mammals (Grebmeier and Harrison, 1992; Lønne and Gabrielsen, 1992).

This work also identified a distinct, and for the Barents Sea unique, Arctic and deep-water faunal taxonomic association prevailing on the Yermak Plateau, north of Svalbard, embedded into Arctic Water below 500 m of depth. This assemblage included a diversity of large arctic shrimps *Hymenodora glacialis* (Havens, 1969), the benthic-pelagic and circum-arctic octopod *Cirroteuthis muelleri* (Collins, 2002) that are long-lived and with a slow recovery and growth, low fecundity and an unknown population trend (IUCN redlist, 2022), the large cold-water amphipods *Eurythenes gryllus* (France and Kocher, 1996) with females

reaching 7.5 cm length before being mature (sealifebase 2022), and *Cleippides quadricuspis* (Piepenburg et al., 1996), and the over 2 m high, upright boreal-polar, slow growing, and up to 75 year old sea-pen *Umbellula encrinus* (de Moura Neves et al., 2018). *U. encrinus* is usually found below 1300 m in waters > 0°C on the Norwegian slope (Gonzalez-Mirelis and Mortensen, 2015) but has a shallower distribution in the Barents Sea north of 77°N (Jørgensen et al., 2016). The morphological analyses weakly identified deep, current rich cold waters to filter large, upright, predatory species such as *U. encrinus*. A possible response to the ongoing ocean warming may be a retraction of the unique bathyal and arctic fauna of the Yermak Plateau into deeper and cooler waters down the slope. Deep-water biodiversity, facing an escalation in climate velocities, need future open-ocean protected areas to optimize opportunities for climate adaptation (Brito-Morales et al., 2020). We therefore suggest the Yermak Plateau to become, not only tentatively closed for bottom trawling (Jørgensen et al., 2020), but a marine protected area towards human activity.

5. Conclusion

We expect that the ongoing rapid Atlantification will have profound consequences for the biodiversity and functioning of the high north Barents Sea ecosystem. On the shelf north of Svalbard flooded by Atlantic Waters, a continued Atlantification may push a fast moving, deposit-feeding association of shrimps and amphipods further east. In the transition shelf-area northeast of Svalbard, this shift may push back flat-bodied, medium size, crawling echinoderms identified with Arctic Water. But because e.g. the commercial *Pandalus borealis* is both an important prey in the marine food web, but also vulnerable to long-term climatic changes, this transition zone should be monitored to follow a possible changing shelf ecosystem. Deeper on the slope, the Atlantification could facilitate for increased sponge grounds and their rich associated fauna, causing an increase in biodiversity and structural habitat. Deeper and more offshore, a taxonomic community are particularly vulnerable toward Atlantification. This includes large, slow-growing, predatory species (e.g. the 2.5 m long seapen *Umbellula encrinus* and the long-lived octopod *Cirroteuthis muelleri* with a low fecundity and a unknown population trend) distributed in the deep, current rich cold waters on the Yermak Plateau north west of Svalbard. This calls for open ocean protected areas to optimize opportunities for climate adaptation for this unique seabed community.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

We acknowledge the valuable data collected in Ecosystem cruises of the Institute of Marine Research (IMR) and the efforts of colleagues and staff on the ships, in the laboratories, and the offices in this regard. Thanks also to the Research Council of Norway for funding SI_ARCTIC (Grant number 228896), TIBIA (Grant number 228880), and The Legacy of Fridtjof Nansen (Grant number 276730) projects that have supported field work and writing of this manuscript. Thanks to the two anonymous referees for editing and providing valuable comments.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.poccean.2022.102792>.

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