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Taxonomic and functional patterns of macrobenthic communities on a high Arctic shelf: A case study from the East Siberian Sea

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ABSTRACT

The Siberian Arctic is one of the regions, where the ongoing climate change is the most evident. There is limited knowledge available on the distribution of macrobenthic communities in the Siberian Arctic, their stability and functional structure. We used data from two latitudinal transects from the East Siberian Sea shelf to describe the distribution of macrobenthic communities as well as to identify the main environmental drivers responsible for the observed patterns. Almost all the studied area was under the direct influence of river runoff. Macrobenthic communities were dominated by the bivalve *Portlandia arctica* and were generally characterised by low species and functional diversity. We suggest that the observed pattern is a direct consequence of considerable river runoff combined with low primary productivity. The overall pattern of macrobenthic distribution corresponds well with the data obtained in the previous decades, suggesting long-term stability of these communities.

1. Introduction

The East Siberian Sea (ESS) remains the least studied among the Siberian seas, especially in terms of benthic macrofauna (Piepenburg et al., 2011). The shallow ESS can be divided into two provinces with western part strongly influenced by freshwater inputs from the large Siberian rivers, while eastern part is under direct influence of Pacific-derived water masses (Semiletov et al., 2005). The Indigirka and Kolyma are the largest rivers on the coast (Gordeev and Rachold, 2003), but they are not the only major source of freshwater as Lena river runoff is advected from the Laptev Sea to the ESS during the periods of cyclonic atmospheric circulation in the region (Steele and Ermold, 2004; Dmitrenko et al., 2008). In the last decades there was a shift in the ice regime of the ESS towards decrease of ice massifs in summer (Yulin et al., 2018), which allowed investigations of previously inaccessible areas.

The ESS is an area of high biogeochemical activity associated with high input of terrestrial organic matter on the west while marine primary production dominates Pacific influenced waters on the east (Anderson et al., 2011). This is reflected in sediment organic matter composition, which has higher contribution of terrestrial organic matter on the western shelf of the ESS, especially close to river deltas (Semiletov et al., 2005; Vetrov et al., 2008). Moreover, massive coastal erosion is a major source of permafrost organic carbon to the ESS shelf (Vonk et al., 2010; Vonk et al., 2012). High input of terrestrial organic carbon and its degradation results in elevated levels of CO_2, which contributes to acidification of coastal waters and, consequently, creates unfavourable conditions for calcifying organisms (Anderson et al., 2011; Semiletov et al., 2016). Despite being recognized as an important area of terrestrial organic carbon sedimentation and mineralization, little is known about macrobenthic communities, inhabiting the shallow ESS. Macrobenthos plays an important role in organic matter mineralization through bioturbation and bioirrigation, however, how pronounced these events are depends on faunal abundance and community structure (Kristensen, 2000; Haese, 2002; Biles et al., 2002). Previous studies of macrofauna found two main communities on the shelf, reflecting hydrological and sediment properties of the shelf: the eastern part is inhabited by an *Ennucula tenuis* community, while sediments in the western part are dominated by the bivalve *Portlandia arctica* var. *siliqua* (Denisenko et al., 2010; Gukov, 2013). However, the role of macrobenthos in carbon cycling on the ESS shelf is yet to be understood, as well as possible shifts in benthic fauna distribution in the changing Arctic associated with increasing runoff, permafrost thawing and water acidification.

Obtaining knowledge on functional aspects of community structure and diversity is an important step for understanding how ongoing

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changes in the Arctic are affecting ecosystem functioning (Degen et al., 2018). For this purpose, biological trait analysis (BTA) is routinely used, which considers biological properties of species as a proxy for their role in a community (Bremner et al., 2006; Bremner, 2008; Degen et al., 2018; Beauchard et al., 2017). However, despite of increasing number of studies with functional approach in benthic ecology, little effort has been made in the Arctic region to understand a link between taxonomic and functional dimensions, as well as to assess functional redundancy of communities (Cochrane et al., 2012; Kokarev et al., 2017; Liu et al., 2019). Functional redundancy, which can be defined as number of species with similar functional role, is an important property of a community defining its robustness in a changing environment (Naeem, 1998; Hooper et al., 2005). Previous studies suggested low functional redundancy for macrobenthic communities on the Siberian shelf (Kokarev et al., 2017; Liu et al., 2019), however, further studies are needed to understand functional aspects of Arctic macrobenthos.

In this study, we used data collected on the shelf of the ESS during September 2017 to describe current state of macrobenthic communities on the Siberian shelf as a continuation of our previous studies (Kokarev et al., 2017). In particular, we aimed to: 1) describe taxonomic and functional aspects of macrobenthos in the study area and 2) relate observed patterns to environmental drivers.

2. Materials and methods

2.1. Study area

Bordered by the New Siberian islands on the West and Wrangel island on the East, the ESS is the largest of the Siberian seas covering an area of 895 10^3 km^2 with the mean depth of only 52 m (Jakobsson, 2002). The shelf slopes gently northwards with the shelf break located at 100 m depth, which is considered a boundary for the shallow ESS (Williams and Carmack, 2015). Samples for the present study were collected on the shelf of the ESS during the 69th cruise of the R/V “Akademik Mstislav Keldysh” in September 2017. Sampling was arranged in two transects along the shelf that started in the vicinity of the Indigirka and Kolyma rivers (Fig. 1, the map was created using Ocean Data View software, Schlitzer (2001)). Two different gears were used for the sampling: the Van Veen grab and the Sigsbee trawl. The summary for the stations is present in the Table 1.

2.2. Grab samples

Three 0.1 m^2 Van Veen grab samples were taken at each station. The sediment from the grab samples was washed through the 0.5 mm mesh size sieve on board and fixed with 6% buffered formalin. In the lab, animals were sorted, identified to the lowest taxon possible, counted and weighed with a precision of 1 mg. In addition, species from the grab samples were assigned to 7 biological traits divided into 28 modalities

Table 1
Coordinates of the sampling locations.

Station	Transect	Date	Latitude °N	Longitude °E	Depth
5598	Indigirka	05.09.2017	71.465	152.8993	13.8
5600	Indigirka	06.09.2017	72.32333	154.5283	20
5602	Indigirka	06.09.2017	73.23333	156.4317	27
5604	Indigirka	06.09.2017	74.08333	158.3333	24.7
5605	Indigirka	06.09.2017	74.86667	160.1683	45
5606	Indigirka	07.09.2017	75.63333	161.9983	48
5612	Kolyma	08.09.2017	74.38333	168.2033	50
5613	Kolyma	08.09.2017	73.33333	166.8	32.5
5615	Kolyma	09.09.2017	72.35167	165.455	27
5617	Kolyma	09.09.2017	71.36267	164.335	22.5
5619	Kolyma	09.09.2017	70.43167	163.0667	17

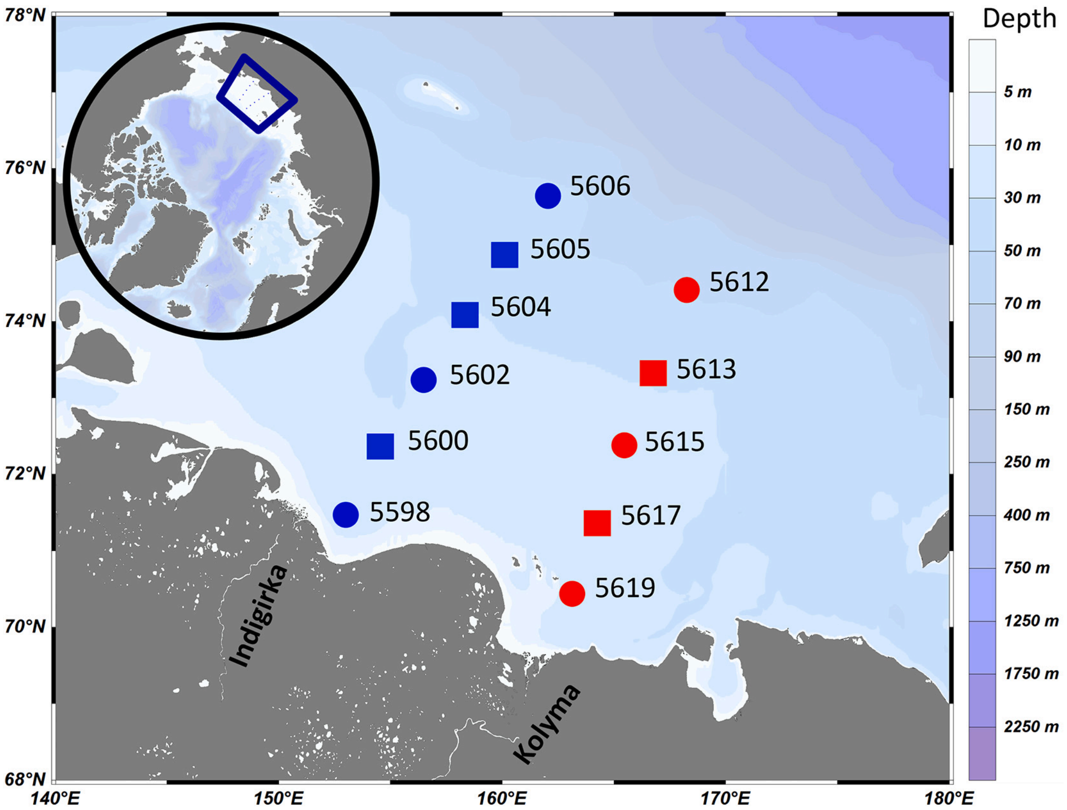

Fig. 1. Map of the study area. Squares are the stations, where both grab and trawl samples were taken; circles are the stations, where only grab samples were taken. Stations are colour-coded according to the corresponding transect: Indigirka (blue) and Kolyma (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

using fuzzy coding approach (Table 2; see Kokarev et al., 2017 for details and references). Diversity indexes were calculated based on pooled abundance data for three replicates, while analyses of taxonomic and functional structure were performed on averaged abundances and biomass per station.

2.3. *Trawl samples*

In addition to the grab samples, Sigsbee trawl samples (2.5 m metal frame width and 0.5 cm mesh size net), were taken at the selected stations (5598, 5602, 5606, 5612, 5615, 5619). The trawl samples were sieved on a cascade of two sieves: 1 mm and 5 mm. In this study, the trawl samples were used only for qualitative analysis of dominant macro/megafauna as a supplement for the grab data.

2.4. *Sediment samples*

The upper 5 cm of sediments were subsampled from a Niemistö gravity corer. Granulometry of these samples was analysed using a laser granulometer “Analizeter-22”. Total organic carbon (TOC) was determined using the dichromate oxidation method.

2.5. *Bottom-water samples*

Temperature and salinity were measured directly with CTD-profiler SBE19 plus (SeaBird Electronics, USA). In addition to temperature and salinity, we measured oxygen saturation, phosphate concentration, nitrate concentration, partial pressure of carbon dioxide as these parameters can be used as indicators of organic matter mineralization (Anderson et al., 2009) and calculated calcium carbonate saturation state both for aragonite (ΩAr) and calcite (ΩCa) as indicators of water acidification (Semiletov et al., 2016).

For the hydrochemical analyses the bottom water layer sampled with a Niemistö gravity corer was used. Samples for determination of pH, nutrients and alkalinity were collected in plastic 0.5 l bottles without preservation and processed on board. In waters with high concentration of particulate matter, samples for nutrient determination were prefiltered through 0.45 μm filters (Millero, 1995).

Dissolved oxygen determination was conducted with standard Winkler method (Parsons, 2013). Technique of nitrate nitrogen determination is based on reduction of nitrates to nitrites and subsequent colorimetry (Parsons, 2013). Phosphates were measured using colorimetric techniques by Murphy and Riley (Parsons, 2013). The pH value (NBS scale) was determined using potentiometric method (Dickson, 1993) on the pH-meter HANNA HI 2210, for calibration we have used appropriate HANNA buffer solutions. Analysis of total alkalinity was conducted by direct titration (the Bruyevich method) with a visual determination of the titration end point (Pavlova et al., 2008), which is comparable with other methods of total alkalinity determination (Dickson and Goyet, 1994; Dickson et al., 2003). Carbonate system parameters such as aragonite saturation (ΩAr) and partial pressure of carbon dioxide (pCO2) were calculated using temperature, salinity, total alkalinity and pH data with “Program Developed for CO2 System Calculations” (Lewis and Wallace, 1998).

Table 2
List of biological traits and related modalities.

Trait	Modality	Code
Maximum size	<1 cm	S1
	1-3 cm	S2
	3-5 cm	S3
	>5 cm	S4
Body design	Vermiform, segmented	BD1
	Vermiform, unsegmented	BD2
	Bivalved	BD3
	Turbinate	BD4
	Articulate	BD5
	Radial	BD6
	Colonial	BD7
Environmental position	Epifauna	EP1
	Infauna	EP2
Mobility	Mobile	M1
	Discretely mobile	M2
	Sessile	M3
Living habit	Tube-dweller	LH1
	Burrower	LH2
	Surface crawler/swimmer	LH3
	Attached	LH4
Feeding habit	Surface deposit	FH1
	Subsurface deposit	FH2
	Carnivore/Omnivore	FH3
	Suspension	FH4
	Symbionts	FH5
Reproduction strategy	Pelagic	RS1
	Short pelagic	RS2
	Benthic	RS3

2.6. *Statistical analyses*

All the statistical analyses were performed in Primer V7 (Clarke and Gorley, 2015) and R software (version 3.6.1; R Core Team, 2019).

Total number of taxa, expected number of species per 50 individuals (ES (50)), Shannon index (using log base 2) and Pielou’s evenness (J’) were used as measures of diversity based on species composition (Clarke et al., 2014). We also used Functional dispersion (Fdis) as a measure of functional diversity, which was calculated using R package FD (Laliberté and Legendre, 2010). Prior to the calculation of Fdis, the “Species x Traits” matrix was standardised using “prep.fuzzy.var()” function in the package ade4. Subsequently, Fdis was calculated in two steps: first, a Gower dissimilarity matrix was calculated using R package ade4, which allows for fuzzy coded data. The resulting dissimilarity matrix was used to calculate Fdis using the package FD. We used Fdis/H′ ratio to assess functional redundancy of the communities: whenever this ratio decreases, the functional redundancy increases (van der Linden et al., 2012). In addition, we performed linear regression of Fdis on H′: a strong linear relationship with a slope close to 1 between the two indicates low functional redundancy (Micheli and Halpern, 2005). Before the regression, indexes were normalised (subtracted the mean and divided by standard deviation).

To assess community structure, we used both abundance and biomass. For species composition, the data were standardised by station and subsequently square root transformed. For functional structure, square root transformed abundance/biomass was multiplied by species affinity for a selected modality, and the resulting matrix “Stations x Traits” was standardised by each trait (Kokarev et al., 2017). The above-described transformations were used to reduce the role of dominant species. Bray-Curtis coefficient (Bray and Curtis, 1957) was used to calculate the dissimilarity matrix for both species and functional community structure analyses. The results were visualised with nMDS using “metaMDS()” function in the package vegan (Oksanen et al., 2019). The environmental factors were fitted on the ordination diagrams using function “envfit()” and the ordinations were compared using function “protest()” in the same package. For the shade plot, species were clustered using index of association: a similarity index, which is calculated as the Bray-Curtis index based on species abundances standardised across samples with values ranging from 0 (perfect “negative” association) to 100 (perfect “positive” association”) (Clarke et al., 2014).

3. Results

3.1. *Environmental setting*

Measured sediment variables showed no pronounced patterns along the transects. The largest TOC value was observed at the station near Indigirka mouth (1.52%), while on the rest of the stations TOC values did not exceed 1% (Fig. 2A). The sediments consisted mainly of fine fractions (Silt+ Clay; Fig. 2B). The highest contribution of sand fraction to sediment composition was observed at the stations close to Kolyma mouth while at the rest of the stations sand content was generally insignificant.

Two main types of the bottom water masses could be distinguished: river-influenced warm (> 0 °C) and less saline (< 30) were distributed on the south while cold (< −1.2 °C) and saline (> 30) prevailed on the northern stations (Fig. 3 AB). Oxygen saturation was high with the lowest value of 74.6% (Fig. 3C). The near bottom waters were generally enriched in CO2 with pCO_2 values over 561 μatm, with the highest values observed at the stations close to the coast (Fig. 3D). Nitrate content increased at the deepest stations (Fig. 3E), while phosphate showed variation in a narrow range (Fig. 3F). Aragonite saturation state (ΩAr) was <1 at all stations (Fig. 3G). Calcite saturation state (ΩCa) showed the same pattern as ΩAr but showed higher values from 0.74 to 1.46. pH ranged from 7.75 to 7.97 (Fig. 3H).

3.2. Univariate characteristics

The stations close to the Kolyma delta (5619 and 5617) showed higher abundance and biomass compared to the shallow stations of the Indigirka transect (Fig. 4 AB). The high latitude stations were characterised by the lowest abundances (< 100 individuals per 0.1 m^2) and biomass (< 1.5 g wet weight per 0.1 m^2). Different patterns for number of taxa were revealed between two transects: along the Kolyma transect it generally decreased with latitude, while along the Indigirka transect there was an increase towards the northmost station 5606 (Fig. 4C). The latter station showed considerably higher levels of Shannon diversity (H′) and ES(50) compared to the rest of the stations (Fig. 4 DE). Except for the stations 5619 and 5617, evenness (J’) was increasing with latitude (Fig. 4F). Both transects showed an increase in functional dispersion followed by decrease and subsequent increase (Fig. 4G). The ratio Fdis/H′ was higher along the Indigirka transect (Fig. 4H). The results of linear regression between functional (Fdis) and taxonomic diversity (H′) showed only a moderate linear relationship: three stations with the highest functional diversity (5604, 5617, 5606) had considerable variation in levels of species diversity (Fig. 5).

Only a few of univariate characteristics of macrobenthos were significantly ($p < 0.05$) correlated with measured abiotic parameters. Abundance and biomass were negatively correlated with salinity ($r = -0.604$ and $r = -0.681$, respectively), while only biomass was positively correlated with temperature ($r = 0.761$). Number of species was positively correlated with sand content ($r = 0.777$) highlighting the relatively high number of taxa at the stations 5619 and 5617 with high sand content in the vicinity of the Kolyma delta. Among other diversity estimates only evenness (J’) showed a clear linear relationship with abiotic variables, including depth, temperature and nitrate ($r = 0.728$, $r = -0.624$ and $r = 0.650$, respectively).

3.3. Community structure

Overall, 94 taxa were recorded in the grab samples, of which 33 were rare (present only in 1 grab sample). 72% of the total individuals belonged to one species, the bivalve *Portlandia arctica*, while other species were poorly represented (less than 5% of the total abundance). Only 4 species contributed to 86.5% of the total biomass: previously mentioned *P. arctica* (38.1%), the bivalve *Astarte borealis* (20.8%) and two isopod species *Saduria sabini* (15.3%) and *Saduria sibirica* (12.2%).

Results of several parallel ordinations did not reveal any generalised pattern of communities on the ESS shelf (Fig. 6). However, the station 5606 differed from the rest of the stations on all the ordination diagrams, while the station 5619 had a distinct functional composition based on biomass. The axes of nMDS based on species biomass were correlated only with depth and sand content, while axes of nMDS based on species abundances were correlated with depth and nitrates concentration in the bottom water (Fig. 6 AC). Ordinations based on functional composition did not show any significant relationships with measured environmental variables (Fig. 6 BD).

Results of protest routine showed that two ordinations based on species composition were highly correlated but results of two different ordinations based on functional composition were also comparable (Table 3). However, biomass-based ordination of functional composition yielded different results from biomass-based ordination of species composition.

Most of the stations, excluding 5606, could be typified by the dominance of the bivalve *Portlandia arctica* both in terms abundance and biomass (Fig. 7 AB). Another common large species was the isopod *Saduria sabini*, while the bivalves *Astarte* spp. were present only on the station 5619 (Fig. 7A). Polychaetes *Micronephtys minuta*, *Aglaophamus malmgreni*, Cirratulidae gen. spp. and the bivalve *Ennucula tenuis* were among common taxa but showed no clear distribution pattern (Fig. 7B). As taxonomic and functional structures were correlated, traits composition reflected mainly the traits of a few dominant species. Based on abundance, the most common combination of traits was medium sized bivalved mobile burrowing surface deposit feeders with short-pelagic reproduction stage (S2 + BD3 + M1 + LH2 + FH1+ RS2), while based on biomass large carnivore articulate surface crawlers were also common (S4 + BD5 + LH3 + RS3). The only exception was station 5606, where segmented worms (BD1) and subsurface deposit-feeders (FH2)

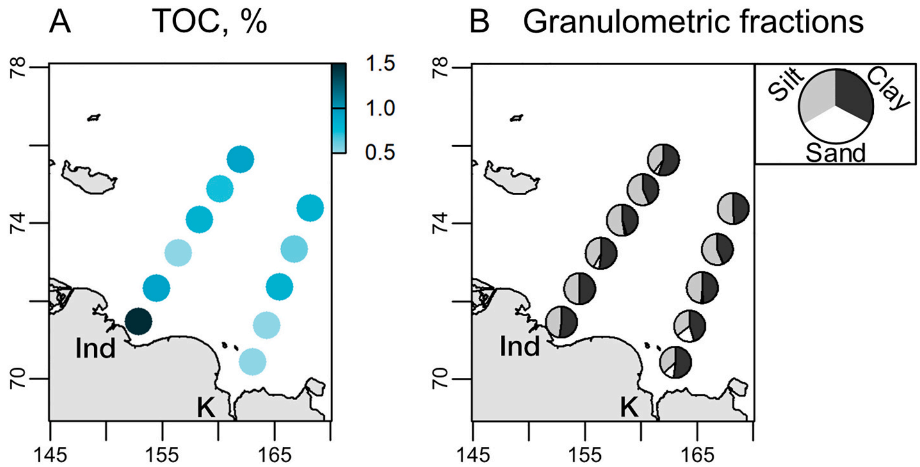

Fig. 2. The sediment characteristics along the two transects. A— total organic carbon (TOC), %. B – contribution of the main granulometric fractions to the sediment composition: Silt (< 0.005 mm), Clay (0.005–0.05 mm) and Sand (> 0.05 mm).

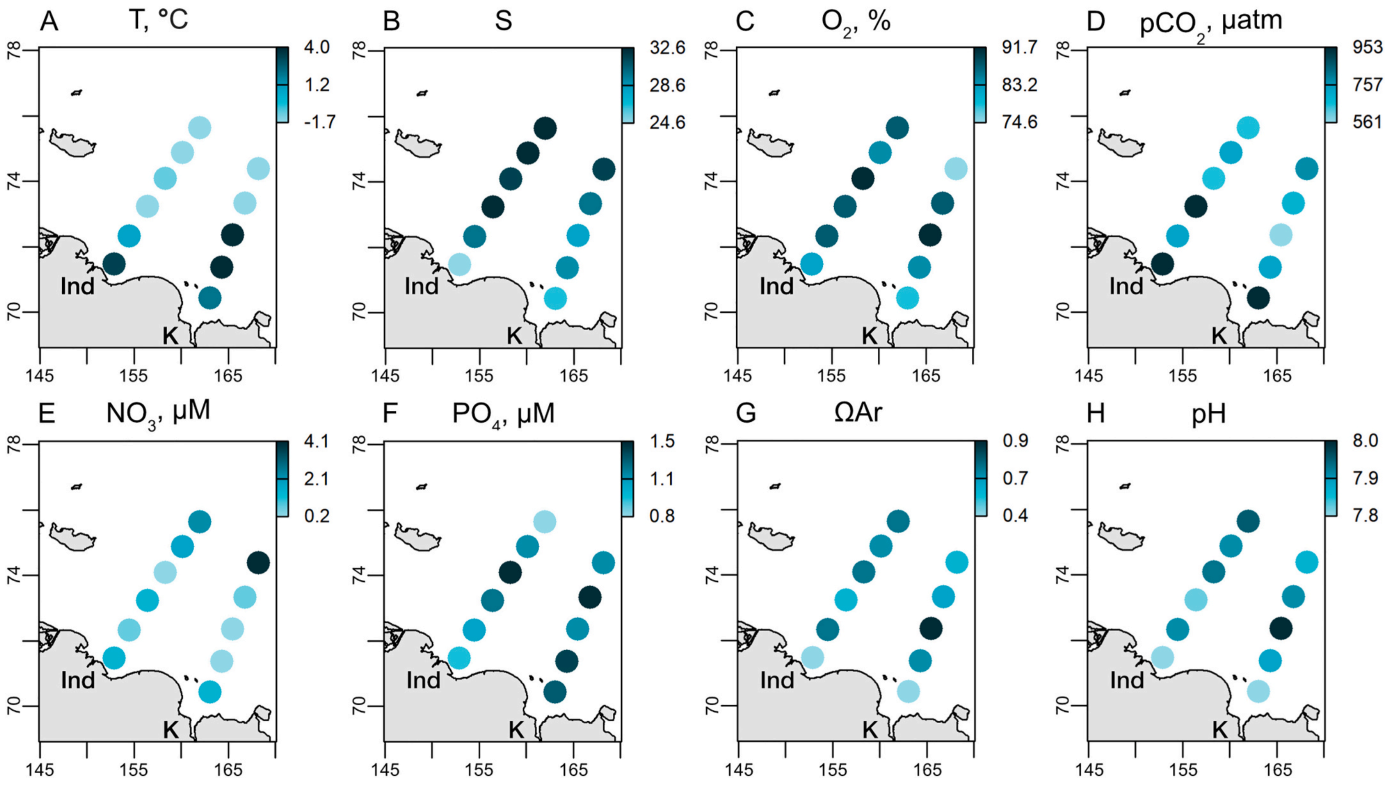

Fig. 3. Hydrochemical characteristics of the bottom water layer. A— temperature (T), °C; B—Salinity (S); C – oxygen saturation (O_2), %; D— partial pressure of carbon dioxide (pCO2), µatm; E—nitrate concentration (NO_3), µM; F—phosphate concentration (PO_4), µM; G— aragonite saturation state (ΩAr); H— pH.

had significant contribution, while short-pelagic reproduction strategy was absent. The station 5619 was the only one that had high dominance of medium-large suspension feeders based on biomass.

3.4. Trawl samples

Trawl samples showed a similar trend along two transects with increasing contribution of the gastropod *Colus sabini*, the sea star *Urasterias lincki* and the isopod *Saduria sabini* and decreasing role of the bivalve *Portlandia arctica* and the isopod *Saduria sibirica* northwards (Fig. 8). Two stations closest to the river deltas from two transects differed significantly: the station 5619 had high abundances of the bivalves *Astarte* spp. and the sea star *Leptasterias groenlandica,* while the station 5598 was typified only by *P. arctica* and *S. sibirica*. The ophiuroid *Ophiocten sericeum* was recorded only at the station 5606.

4. Discussion

Our data reveal that the shelf of the East Siberian Sea is inhabited by a species poor macrobenthic community dominated by the bivalve *Portlandia arctica* except for the northmost station 5606. Excluding stations 5619 and 5617, there was a general increase in evenness along the transects northwards, which indicated a decrease of *P. arctica* dominance associated with colder, more saline and nitrate-rich water masses. Trawl samples confirmed the importance of *P. arctica*, as well as of isopods *Saduria spp.,* which are poorly represented in grab samples due to their large size. This pattern is very similar to the dominance of *P. arctica* and *Saduria spp.* (in the trawl samples) on the Kara sea shelf near the large estuaries of the Ob and Yenisey rivers (Galkin and Vedenin, 2015; Vedenin et al., 2015) and the areas east to the Lena delta in the Laptev Sea (Petryashov et al., 2004; Kokarev et al., 2017). While in the other Siberian seas these *P. arctica* communities are limited to areas close to deltas/estuaries, in the present study it occupied almost all the study area, excluding station 5606, where no *P. arctica* was observed, and station 5612, where abundance of *P. arctica* considerably decreased. This suggests that the disturbance caused by fluctuations in salinity and sedimentation of riverine particulate matter influences larger area on the ESS shelf. Stations close to the Kolyma delta were characterised by the highest number of taxa recorded with the station 5619 dominated by suspension feeding bivalves *Astarte* spp. in addition to *P. arctica* based on biomass. Suspension feeding is a trait correlated with higher near bottom velocities (Pisareva et al., 2015; Rand et al., 2018), which are also indicated by the highest sand content in the sediment composition among the studied stations. Most probably, this results in lower sedimentation rates, also indicated by lower TOC values compared to stations close to the Indigirka delta, which has a positive effect on species and functional diversity.

The ophiuroid *Ophiocten sericeum*, which is an indicator of the Arctic shelf macrobenthic communities not influenced by river runoff (Petryashov et al., 2004; Galkin and Vedenin, 2015; Vedenin et al., 2015), was present only on the station 5606. This station was different in having higher proportion of vermiform subsurface deposit feeders, however, unlike other areas of the Arctic shelf, not influenced by river runoff or enhanced sedimentation, the numbers of tube-dwelling taxa were low (Cochrane et al., 2009, 2012; Kokarev et al., 2017). Tube-dwelling taxa, represented in the high Arctic mainly by oweniid and maldanid polychaetes, can be considered as a sign of "mature" and diverse communities that support high rates of organic matter mineralization (Zaborska et al., 2018). Contrary, *P. arctica* is characteristic of an early stage of community succession in areas with high sedimentation rates (Syvitski et al., 1989). The observed pattern on the ESS shelf suggests that the environmental setting in the area hampers development of more functionally diverse communities, even in the northmost areas.

While evenness generally increased along transect, total abundance and biomass were negatively correlated with salinity. Most probably this link is not direct, as more northern stations are characterised not only by higher salinities, but also longer period of ice-coverage and, thus shorter

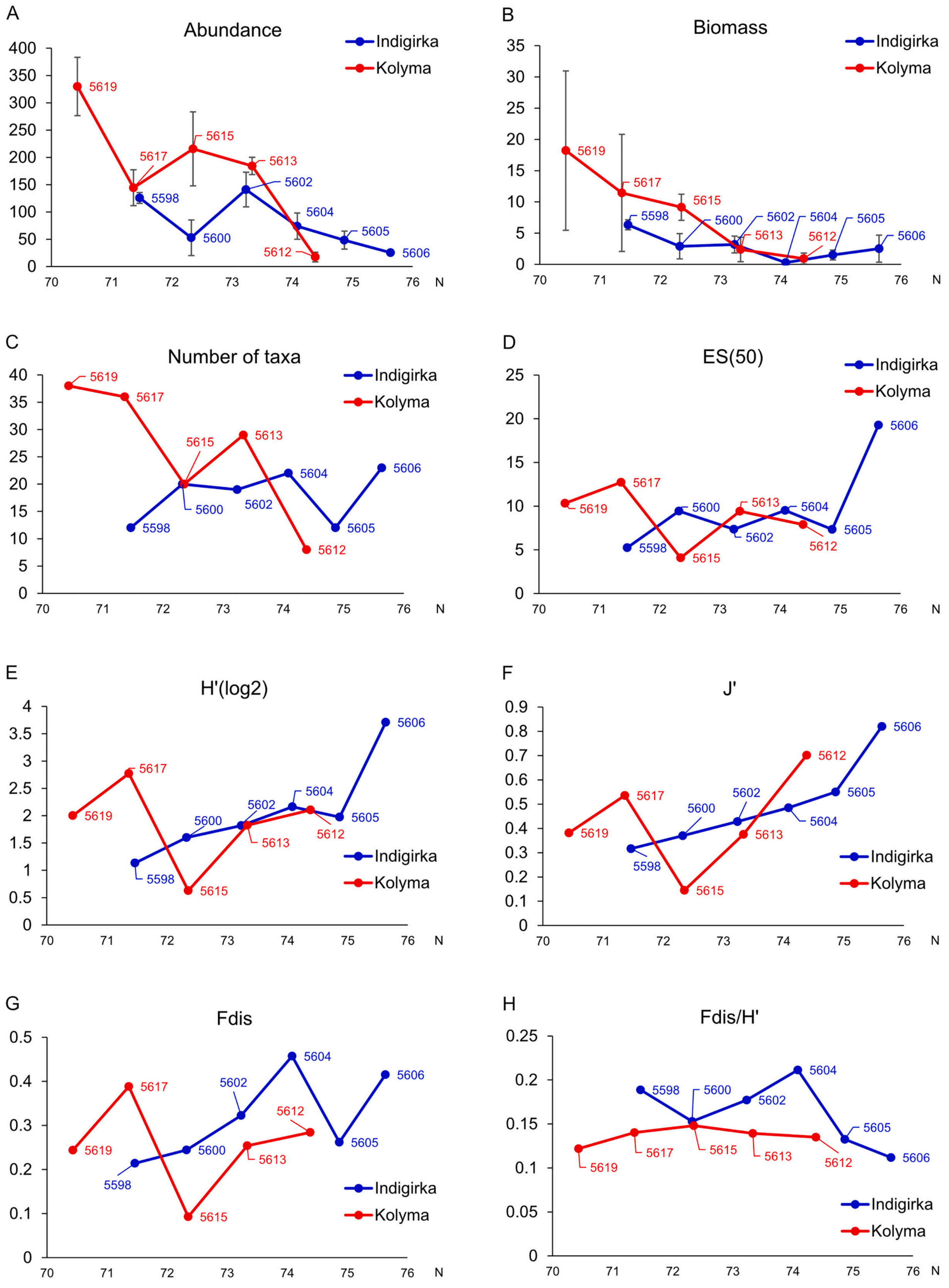

Fig. 4. Macrofaunal characteristics of the two transects. A – total abundance, ind/0.1 m^2; B – total biomass, g/0.1 m^2; C – number of recorded taxa; D – expected number of species per 50 individuals, ES(50); E – Shannon' diversity index, H′(log2); F – Pielou's evenness, J'; G – functional dispersion, Fdis; H – functional redundancy, Fdis/H′.

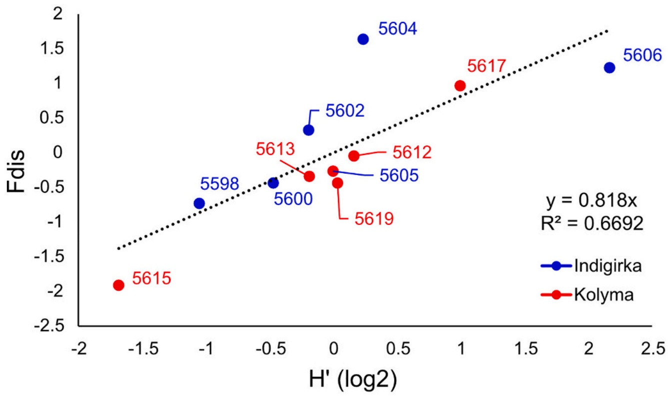

Fig. 5. Relationship between Fdis and H′ values, and results of linear regression. Indexes were normalised (subtracted the mean and divided by standard deviation).

vegetation period, which could lead to lower carbon export of marine primary production to the seafloor (Wassmann et al., 2004). The northmost station 5606 had abundance several times lower compared to northern Laptev sea shelf (250 individuals per m^2 compared to previously reported 1559 by Petryashov et al. (2004) and 1980–3320 by Kokarev et al. (2017). Net primary production of the ESS is generally lower compared to the Laptev sea (Arrigo and van Dijken, 2015). The extreme oligotrophic conditions were also evident from direct measurements of the primary production during the cruise (Demidov and Gagarin, 2019). This implies that low primary production is a limiting factor for species rich and abundant community to develop. A link between primary production and abundance, as well as species richness, was previously showed for the Barents Sea shelf (Cochrane et al., 2009). Previous studies in the ESS indicated that biomass of calcifying organisms was the lowest where ΩAr was the lowest and pCO2 was the highest (Semiletov et al., 2016), suggesting state of acidification as an important factor for distribution of a bivalve-dominated community. In our study, the lowest values for ΩAr and ΩCa as well as the highest values for pCO2 were observed on the shallowest stations 5598 and 5619, where highest values of biomass were observed for the two transects. Thus, no specific

Table 3
Procrustes correlations from protest routine between different ordination diagrams. Significant correlations are in bold.

	Biomass/functional	Biomass/species	Abundance/functional
Biomass/species	0.4361, p = 0.269		
Abundance/functional	**0.6675, *p* = 0.012**	0.562, p = 0.072	
Abundance/species	0.4371, p = 0.307	**0.8564, *p* = 0.001**	**0.6317, *p* = 0.028**

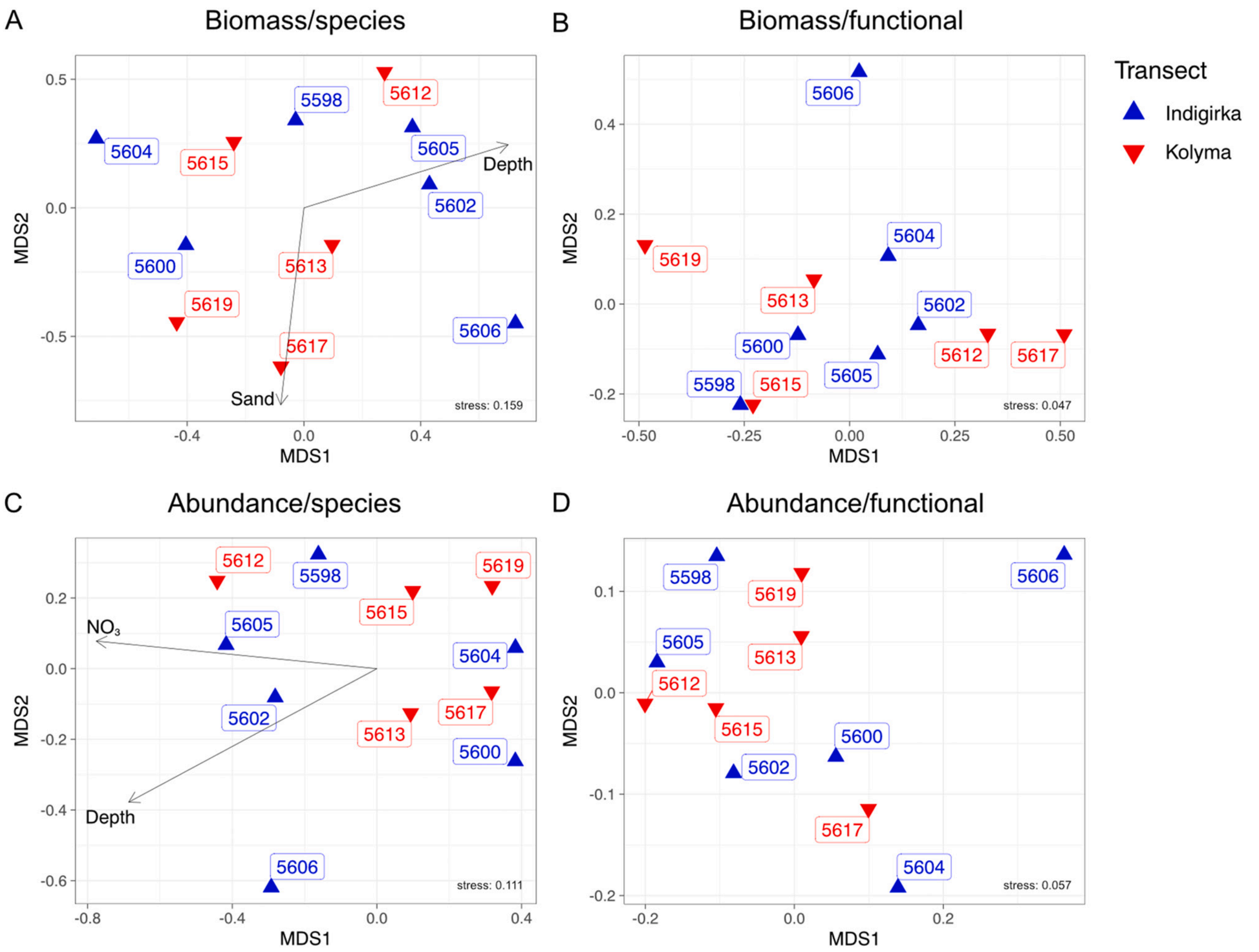

Fig. 6. Results of nMDS ordination with fitted vectors of environmental variables ($p < 0.05$). A – ordination diagram based on transformed biomass of species, B—ordination diagram based on biomass-weighted traits composition, C – ordination diagram based on transformed abundance of species, D – ordination diagram based on abundance-weighted traits composition. For data transformations see section 2.6.

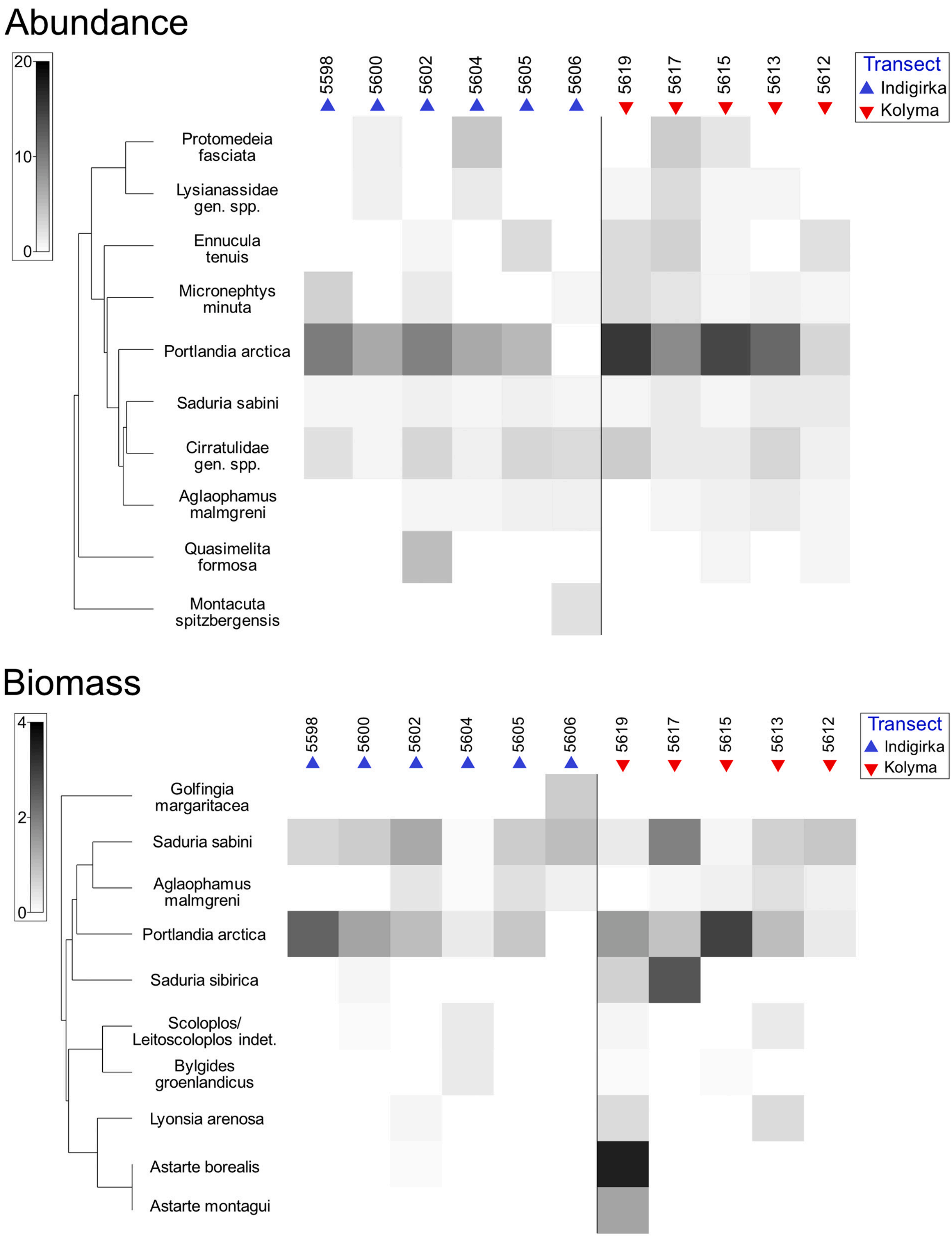

Fig. 7. Shade plot of the species distribution along two transects based on square root transformed abundance and based on square root transformed biomass (average for 3 0.1 m^2 replicates) . Species are clustered using UPGMA clustering based on index of association. The stations are presented according to the order on the transect from the south to the north.

response to indicators of ocean acidification was observed on a community level in our study; most probably its effects are overridden by low productivity and river runoff.

Previous studies in the Arctic suggested strong linear relationship between taxonomic and functional diversity, indicating low functional redundancy of these communities (Kokarev et al., 2017; Liu et al., 2019). In this study, the relationship was not linear, on contrary, indicating high functional redundancy, as increase in species diversity

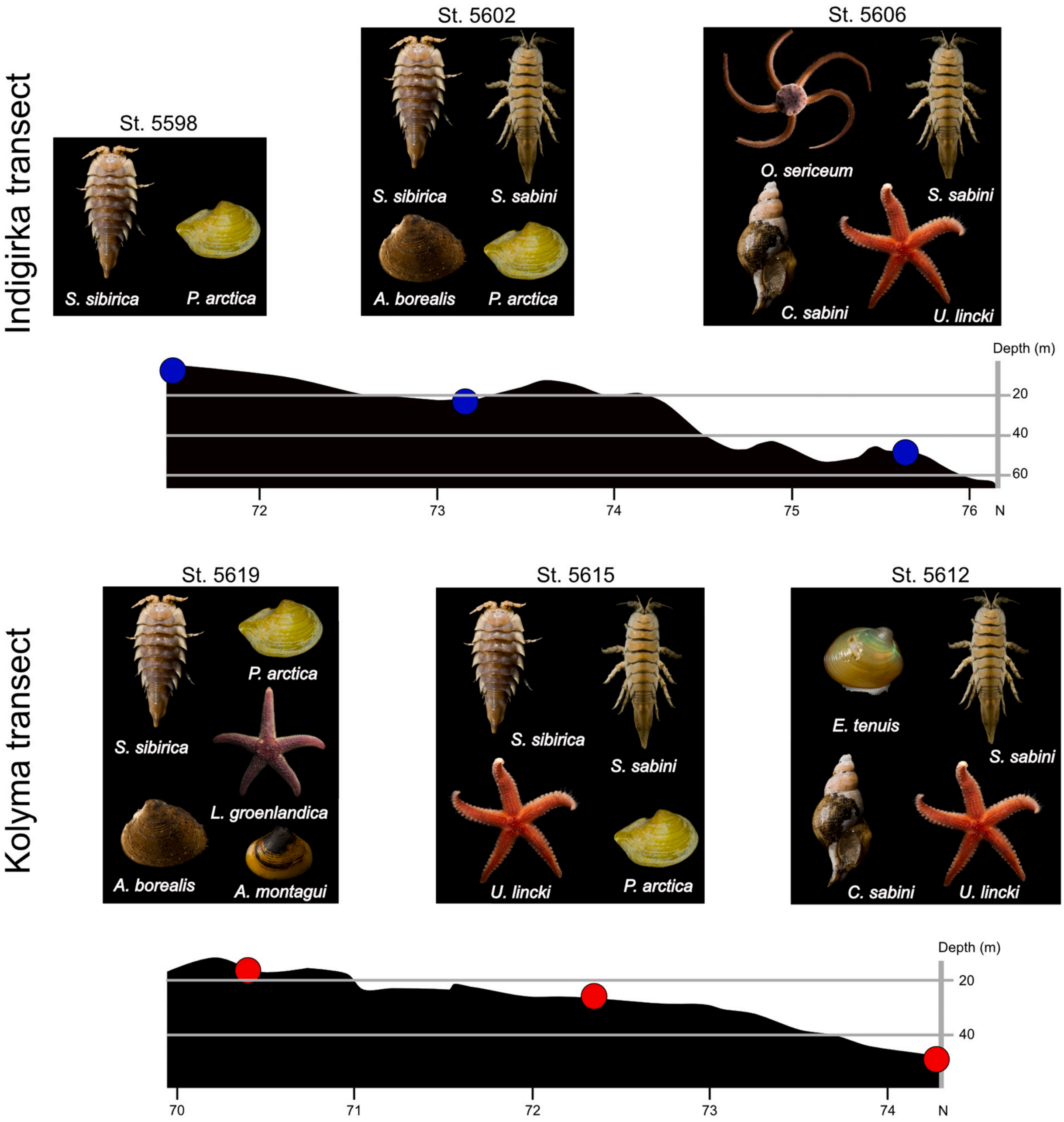

Fig. 8. Distribution of dominant species along two transects based on trawl samples. The following taxa are presented: *Saduria sibirica*, *Portlandia arctica*, *Astarte borealis*, *Astarte montagui*, *Leptasterias groenlandica*, *Saduria sabini*, *Urasterias lincki*, Colus Sabini. Photos by A. Vedenin.

reaches a limit in functional diversity, suggesting the species pool on the ESS consists of functionally similar species (Micheli and Halpern, 2005). On the other hand, the overall low species richness of the studied area makes it more of an exception, than a rule for Arctic shelf macrobenthos. Considerable river runoff combined with low primary productivity create an unstable environment for macrobenthos that selects for particular traits of macrobenthos, represented by a few species that can adapt to such severe conditions. Indeed, with comparable sampling size in the Laptev sea, 197 taxa were recorded compared to 94 in the present study (Kokarev et al., 2017).

Overall, the main structuring factors for macrobenthic communities on the western part of the ESS shelf are considerable river runoff and oligotrophic conditions resulting in taxonomically and functionally impoverished communities, even in the northmost parts of the shelf. These communities are rather simply organized: mobile surface deposit feeders, such as *P. arctica*, might rely, in part, on microbially-degraded terrestrial organic matter as a carbon source (Dunton et al., 2012), while large mobile carnivores, such as *Saduria spp*., prey on this deposit-feeding fauna (Ejdung and Bonsdorff, 1992). Considering general absence of deep burrowing subsurface deposit feeders and tube-dwellers, that would contribute to functional diversity, it may be assumed that macrobenthos contribution to benthic functioning is limited. The distribution of dominant species corresponds to previous surveys conducted in the region up to the year 2004 (Denisenko et al., 2010), suggesting the stability of these communities. However, considering its extremely low species richness, it is unclear how the bottom ecosystem of the western ESS will be affected by future climatic changes: while increasing primary production and decreasing ice-cover in the Arctic can lead to developing of more diverse communities in the northern part, the increase in the river runoff and coastal erosion will lead to higher sedimentation rates, that, on contrary, might negatively affect benthic communities. Thus, more monitoring studies are needed to understand the possible vectors of change.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2021.102078.

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