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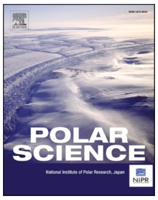

Franz Josef Land’s macrobenthos: Record-high wet biomass values on the Eurasian Arctic shelf

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ABSTRACT

To address critical gaps in our understanding of benthic ecosystems in the Arctic, this study sampled macrobenthos across the Franz Josef Land archipelago during the 2020–2021 field campaign. In total, 65 benthic grab stations were analysed, and 29 stations assessed for macrofauna with ROV video recordings. The stations, located in shallow waters ranging from 11 to 176 m depth, covered a substantial portion of the archipelago. This data set is by far the largest published on the area’s benthic biodiversity since the 1970s. From 143,577 specimens of macrobenthos analysed, a total of 333 taxa (257 species) were identified. Most stations were dominated by three overlapping macrobenthic assemblages: (1) *Strongylocentrotus* sp. – *Ophiura robusta*, (2) *Hiatella arctica* – *O. robusta* and (3) *Astarte* spp. Exceptionally high biomass of macrobenthos was noted, reaching 3.9 kg m^{-2}, possibly the highest documented for the Eurasian Arctic shelf. This finding suggests a greater potential for carbon sequestration in this region than previously understood. High spatial heterogeneity and high benthic biomass can be attributed to the complex hydrodynamic regime and abundance of hard substrates in these shallow waters, which also makes the area attractive for benthic predators, in particular the Atlantic walrus (*Odobenus rosmarus rosmarus*).

1. Introduction

Benthic communities play a crucial role in carbon cycling and sequestration, directly burying carbon in seafloor sediments and processing organic matter, which modulates both immediate and long-term carbon storage (Muller-Karger et al., 2005; Farrelly et al., 2013; Cartapanis et al., 2018). However, estimates of carbon storage in the Arctic Ocean are extremely scarce, with only a few recent studies, such as those by Bourgeois et al., 2017, Armstrong et al. (2019) and Wiedmann et al. (2020), attempting to develop a comprehensive carbon budget for the region. A deeper understanding of the distribution, biomass, and composition of seafloor communities is essential for accurately estimating benthic standing stocks in the Arctic, thereby underpinning any evaluations of the blue carbon potential in Arctic marine ecosystems. Interestingly, a recent study by Sen et al. (2024) suggests that the capacity of Arctic benthos to process increased carbon influxes can lead to additional sedimented carbon being utilised rather than accumulated under warming climate conditions, thereby diminishing the Arctic’s role as a global carbon sink.

Arctic benthos act as long-term indicators of changes in environmental conditions (CAFF, 2013; CAFF, 2017). Typically, macrobenthic invertebrates retained by a 1.0-mm-mesh sieve are used in ecological monitoring, in contrast to the smaller meiobenthic organisms that have shorter life spans, different ecological functions, and require different sampling techniques (Mare, 1942). The Circumpolar Biodiversity Monitoring Programme (CBMP) classifies macrobenthos as focal

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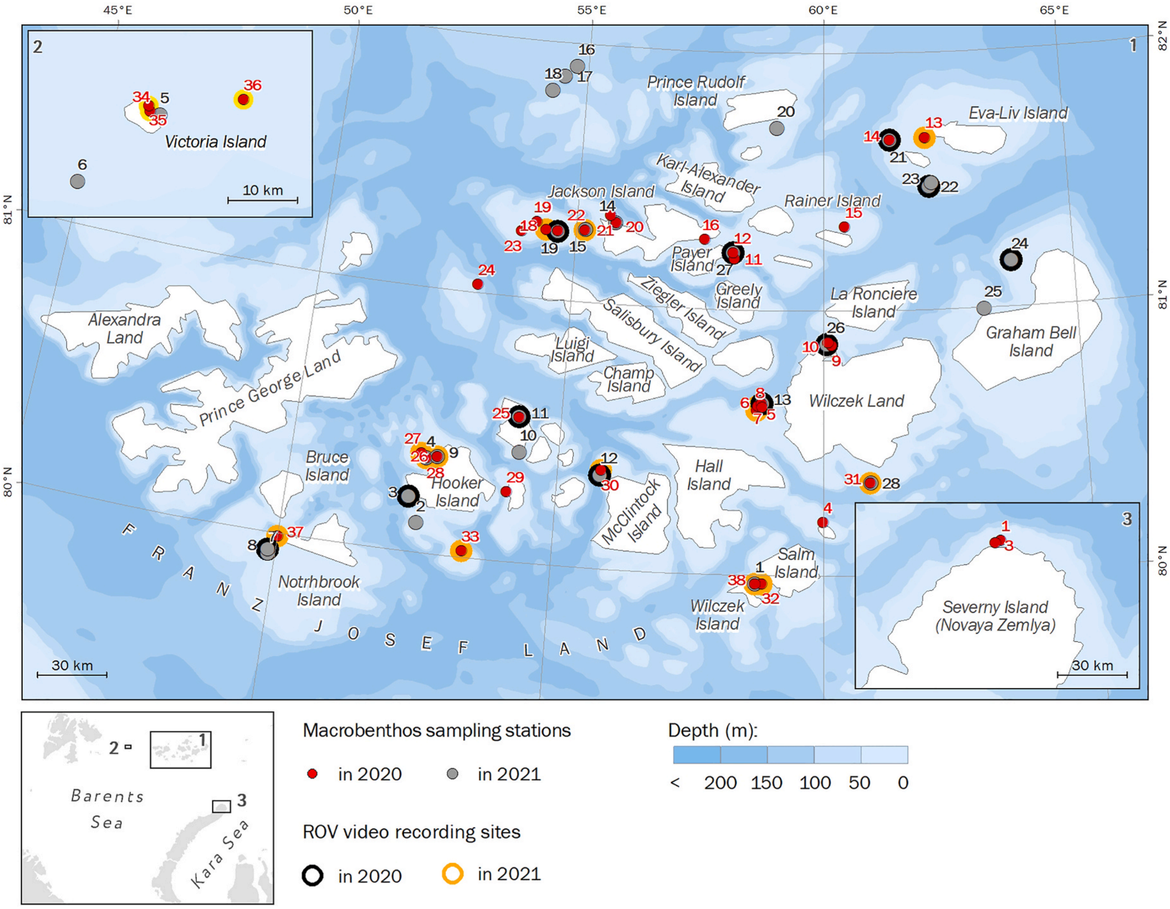

Fig. 1. Overview map of the study area with the marked locations of grab sampling sites and sites of ROV video recordings in 2020–2021.

ecosystem components due to their importance as foraging resources for benthic predators (CAFF, 2017). This study focuses on macrobenthos, or macrofauna, which, in this context, are defined as organisms larger than 0.5 mm (as this was the mesh size used for field sample collection) and visible to the naked eye in ROV video recordings.

Franz Josef Land, located in the northern Barents Sea, is a remote archipelago encapsulated by fast ice most of the year (Dahle et al., 2009). The oceanographic conditions in the research area are known to be heterogeneous due to the presence and mixture of water masses of Atlantic and Barents Sea origin, also supported by the complex seafloor topography with vast shallow-water areas supporting turbulent mixing of the water column, and coastal topology of the archipelago with numerous straits and fjords (Govorukha, 1968; Dvoretsky and Dvoretsky, 2024). The archipelago is designated as an Ecologically and Biologically Significant Marine Area by both the Convention on Biological Diversity (CBD, 2024 – North-eastern Barents–Kara Sea EBSA) and the Arctic Council (AMAP/CAFF/SDWG, 2013), serving as critical habitat for Atlantic walruses and a variety of seabirds. Despite its ecological importance, data on the region's marine ecosystems, especially benthic invertebrates — a primary food source for walruses — are limited (Dvoretsky and Dvoretsky, 2024). While the Barents Sea is among the most studied Arctic shelf seas, with continuous observations from the beginning of the 20th century, research has traditionally focussed on central or transboundary areas relevant to fisheries, often overlooking Franz Josef Land. The majority of data on macrobenthos of Franz Josef Land archipelago were collected during the research expeditions in the 1970–1990s and focused on the shallow waters (up to 40 m) (Golikov and Averintsev, 1977; Averintsev and Pogrebov, 1990; Weslawski and Zajaczkowski, 1992; Luppova et al., 1993; Anisimova, 2001).

A study by Dahle et al. (2009) based on 9 stations sampled in 1992, covered deeper areas of this archipelago up to 312 m deep, finding wet benthic biomass significantly higher than average Barents Sea values, with the highest recorded at 2146 g wet weight m^{-2} (Dahle et al., 2009). Key contributors to this biomass include bivalve molluscs *Hiatella arctica* and *Astarte elliptica* (Dahle et al., 2009). The most recent published data correspond to the surveys conducted in 2006 and 2007, that revealed a noticeably lower wet weight biomass of macrobenthos with a maximum value of 1896 g m-^{2} and a mean value of 428 g m^{-2} (Dvoretsky and Dvoretsky, 2024).

Despite previous research, substantial gaps in our understanding of the region's benthic biodiversity persist, also highlighted in a recent review by Dvoretsky and Dvoretsky (2024). One of the primary limitations is the outdated nature of available data, with most recent studies relying on samples collected over 20 years ago. Another limitation is the lack of focus on mobile megafauna, which can have an important role in benthic ecosystems, especially considering the recent and ongoing expansion of the snow crab *Chionoecetes opilio*, an invasive benthic predator in the Barents Sea (Bakanev, 2015; Gebruk et al., 2021a; Bakanev and Pavlov, 2023). Finally, there is a lack of supporting environmental data, which are crucial to provide context to observed biological processes.

During the RV *Ivan Petrov* expeditions to Franz Josef Land in 2020–2021 to study the populations of Atlantic walruses *(Odobenus rosmarus rosmarus)* and polar bears (*Ursus maritimus*) at the archipelago, an extensive benthic survey was conducted, sampling a total of 65 benthic stations. One of the main goals of the expedition was to tag walruses with satellite linked transmitters to study their movement. A recent publication by Solovyova et al. (2024) presents the results of satellite telemetry study, and it also includes a high-level overview of

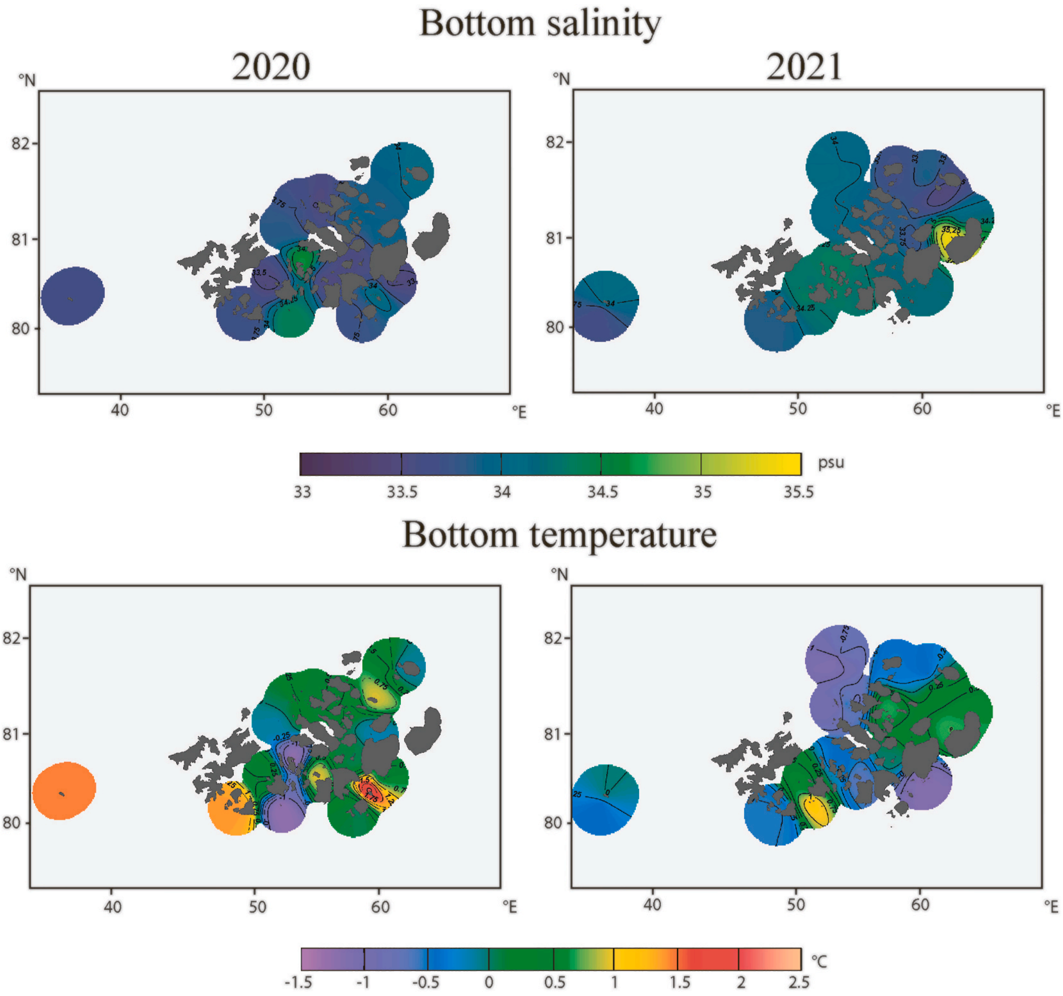

Fig. 2. Near-bottom value of salinity and temperature across the research area as recorded by the CTD profiler (RBR Concerto 3 in 2020, and CastAway CTD in 2021).

available foraging benthic biomass in the area. In contrast, this study analyses the entire benthic dataset, investigating the taxonomic composition, abundance, biomass, and productivity of macrobenthic assemblages. Additionally, our work examines benthic habitats and introduces environmental data from the sampling stations, aspects which have not been explored in other publications.

The aims of this study were (1) to review the present state of macrobenthos in Franz Josef Land archipelago based on the extensive grab sampling campaign in 2020–2021; (2) to characterise benthic macrofauna and habitats based on the ROV video recordings; (3) to characterise variability of macrobenthos and to compare it with that of seafloor habitats; (4) to characterise oceanographic conditions in the area.

2. Methods and data

2.1. Research area and samples collection

2.1.1. Benthic samples

The samples of macrobenthos were collected during the RV *Ivan Petrov* field campaigns to Franz Josef Land archipelago in 2020 (22/08/2020–08/09/2020) and 2021 (13/08/2021–09/09/2021). The research area covered the majority of the archipelago, the sampling sites were chosen in proximity to the known locations of the walrus haul-out spots on the islands (Fig. 1). In addition, water areas near Victoria Island to the west of the archipelago, three open-water control sites to the north of the archipelago, and two sites north of Novaya Zemlya archipelago have been sampled for comparison. In total, 65 sites have been sampled and 195 samples of macrobenthos analysed at the depth range from 11 m to 176 m. Samples were taken with *Van-Veen* or *Okean* benthic grabs with a capture area of 0.1 m^2 in three replicates for each station.

List of stations with coordinates, dates of sampling and depth is available in Appendix 1. The full benthic data set is published in PANGAEA data repository, divided into two data publications on macrobenthic abundance (Kokorin et al., 2024a) and biomass (Kokorin et al., 2024b), respectively.

2.1.2. Environmental data

Depth, temperature, and salinity were measured at each station with the CTD profiler (*RBR Concerto 3* in 2020, and *CastAway CTD* in 2021). The near-bottom salinity and temperature values for each station are available in the associated data publication in data repository PANGAEA (Gebruk et al., 2024).

2.1.3. ROV video recordings

Underwater video transects were carried out with remotely operated vehicle (ROV) *RB-300* at shallow water stations (up to 70 m depth) to characterise macrobenthos and benthic habitats. The ROV was equipped with two servo-driven video cameras (Super HAD 2 CCD; Sony, Tokyo, Japan), with tilt ±90, a lighting complex synchronised with the camera (with 4 light-emitting diodes of 700 Lumens each spaced 10 cm apart), and a navigation system (with a course detector and depth sensor). The video transects were carried out for approximately 7–10 min at 17

Table 1
List of macrobenthic sampling stations with coordinates, depth, near-bottom temperature and salinity according to CTD data.

Site	Lat, N	Lon, E	Depth, m	Bottom temperature, °C	Bottom salinity, PSU
20_01	77.03186167	67.80372333	35	1.342	34.55
20_03	77.02602833	67.706455	23	1.194	34.62
20_04	80.19872	59.98416833	35	2.226	34.25
20_05	80.61891667	58.71873333	18	−0.039	33.43
20_06	80.63376167	58.733205	22	0.592	33.34
20_07	80.64381667	58.805475	27	0.183	33.51
20_08	80.62919167	58.82254333	45	−0.364	33.91
20_09	80.86570167	60.15205333	40	−0.348	33.9
20_10	80.877845	60.07828833	32	0.064	33.96
20_11	81.19308667	58.21064	51	−0.045	34
20_12	81.21651333	58.18092333	18	0.430	33.86
20_13	81.66253167	62.09655333	23	−0.243	34.13
20_14	81.65618667	61.36952167	11	0.695	33.89
20_15	81.32176667	60.4179	33	0.957	33.89
20_16	81.26481	57.601375	21	0.830	33.86
20_17	81.26308833	54.62398167	30	0.127	33.86
20_18	81.26556833	54.39414	23	0.154	33.67
20_19	81.29167333	54.18970833	26	0.419	33.57
20_20	81.31233333	55.78796667	32	0.308	33.6
20_21	81.33777667	55.67423333	28	0.503	33.45
20_22	81.27584667	55.17532167	32	0.655	33.31
20_23	81.250965	53.89932667	37	−0.155	33.85
20_24	81.02986667	53.14055	49	−0.114	33.84
20_25	80.54351167	54.19668167	176	−1.325	34.72
20_26	80.36400333	52.72884667	49	−0.447	33.89
20_27	80.36930333	52.42329167	35	0.440	33.49
20_28	80.35356	52.52526333	41	1.217	33.19
20_29	80.25858333	54.08108333	71	−0.859	34.31
20_30	80.36733	55.812265	36	1.001	33.49
20_31	80.34505	60.87500833	37	0.466	33.44
20_32	79.96729333	58.86829167	31	−0.531	34.11
20_33	80.021675	53.36647	50	−1.277	34.42
20_34	80.16658333	36.75715	25	1.480	33.47
20_35	80.17260167	36.73455333	14	1.479	33.74
20_36	80.223015	37.28641167	51	1.492	33.7
20_37	79.98725667	50.00219167	25	1.403	33.72
20_38	79.96712833	58.74137833	34	−0.188	33.82
21_01	79.96712833	58.73971167	25	0.966	33.34
21_02	80.10737	52.47343	16.5	1.40	34.20
21_03	80.20275	52.28246667	32.0	0.50	34.40
21_04	80.35307333	52.529445	33.5	1.27	34.25
21_05	80.16635	36.8234	75.0	0.10	34.20
21_06	80.04833333	36.48668333	20.6	−0.50	33.50
21_07	79.93446667	49.85821667	49.3	−0.60	33.50
21_08	79.934145	49.86128	45.2	−0.44	34.15
21_09	80.36354667	52.72934167	54.0	−0.30	34.25
21_10	80.41073333	54.25518333	34.1	−0.12	34.35
21_11	80.54378333	54.19346667	39.4	−0.46	34.33
21_12	80.34885833	55.79208167	54.0	−0.64	34.25
21_13	80.64451667	58.8114	63.3	0.05	34.15
21_14	81.31245	55.78345	49.1	−0.90	33.85
21_15	81.27742333	55.17967667	25.9	−0.21	34.05
21_16	81.90855	54.749	38.9	−0.45	33.86
21_17	81.86573333	54.50176667	64.5	−1.17	34.16
21_18	81.80671667	54.27135	66.4	−1.18	34.10
21_19	81.26191167	54.62456833	75.2	−1.15	34.00
21_20	81.70395	59.01945	21.2	−0.34	33.65
21_21	81.65623333	61.36825	26.1	−0.48	33.90
21_22	81.47111667	62.16265	31.8	0.59	33.45
21_23	81.48628333	62.21181667	28.0	0.00	33.35
21_24	81.17378333	63.75208333	25.0	0.66	34.00
21_25	80.99396667	63.17185	24.7	0.76	35.50
21_26	80.87123333	60.06061667	25.7	0.39	33.70
21_27	81.2168	58.17411667	27.4	0.75	33.80
21_28	80.34505	60.88096667	62.9	−1.13	34.17
20_01	77.03186167	67.80372333	30.5	0.77	33.45

stations in 2020 and 12 stations in 2021.

The map of all research sites, including macrobenthos grab sampling stations and ROV video recording sites is presented in Fig. 1.

2.2. *Samples processing and data analysis*

Samples of bottom sediments from the benthic grabs were rinsed over the 0.5-mm nylon mesh with pumped seawater. All macrobenthic invertebrates from the sediment were pre-fixed in a neutralised 4 % formaldehyde solution. In the laboratory, all samples were washed in freshwater and transferred into 70 % ethanol solution for storage.

Macrobenthic invertebrates were identified with the maximum level of certainty through optical microscopy using regional taxonomic keys (Zhirkov, 2001; Naumov, 2006; Buzhinskaja, 2009; Vassilenko and Petryashov, 2009). All taxonomic names have been standardised using the World Register of Marine Species (WoRMS). All specimens were individually counted and weighted after initial fixation with formaldehyde (wet biomass) with reported accuracy to 0.01 g. Bivalve molluscs and gastropods were weighted with shells.

Mean values ± standard deviations (for stations and across the sampling area) were measured for biomass (g m^{-2}) and abundance (ind. m^{-2}) to characterise macrobenthos. In addition, "relative production" index (P) was calculated as a relationship between biomass and abundance based on average exponent of annual production on body-size for macrobenthic invertebrates following Kucheruk and Savilova (1985) and Clarke and Warwick (2001):

$$P = \left(BA^{-1}\right)^{0.75} \times A$$

Where B refers to biomass, A refers to abundance, 0.75 refers to average exponent of annual production on body-size for macrobenthic invertebrates.

The purpose of "relative production" index is to address input both from abundant but low in biomass species (e.g., small polychaetes) and larger organisms that dominate biomass but occur in samples less frequently (e.g., large gastropod or bivalve molluscs) (Clarke and Warwick, 2001).

Statistical calculations were performed using free software PAST version 4.17 (Hammer and Harper, 2024). To characterise diversity of macrobenthos standard diversity indices were used including dominance, Simpson index and Shannon index (Hammer and Harper, 2024). To assess predicted species richness ($\widetilde{S}$) in the research area, a species accumulation curve was calculated using the Chao-2 type estimator (Hammer and Harper, 2024).

A non-metric multidimensional scaling (nMDS) based on the Bray-Curtis similarity index and a hierarchical cluster analysis based on an unweighted pair group method with arithmetic mean (UPGMA) algorithm with Bray-Curtis similarity index were used to distinguish macrobenthic communities based on "relative production" matrix. A meta-analysis study carried out by Warwick and Clarke (1993) showed that the relative production index is the most relevant measure of the relative ecological importance, particularly for the soft-sediment species, compared to abundance or biomass.

To assess significance of differences between groups of stations, a one-way pairwise analysis of similarities (ANOSIM) analysis was used ($p < 0.05$). Contribution of species to observed differences was assessed using similarity percentage (SIMPER) analysis based on Bray-Curtis similarity measure. Canonical Correspondence Analysis (CCA) and Mantel test performed for the matrix of Euclidean distances for environmental factors and Bray-Curtis similarity index for the biotic data (relative production index) were used to assess the relationship between macrobenthic assemblages and environmental parameters (temperature, salinity, and depth) across various sampling stations.

Video recordings were viewed in QuickTime Player (version 10.5) and assessed to identify and count all fauna observable by the naked eye. A taxonomic catalogue was compiled and identifications to the lowest

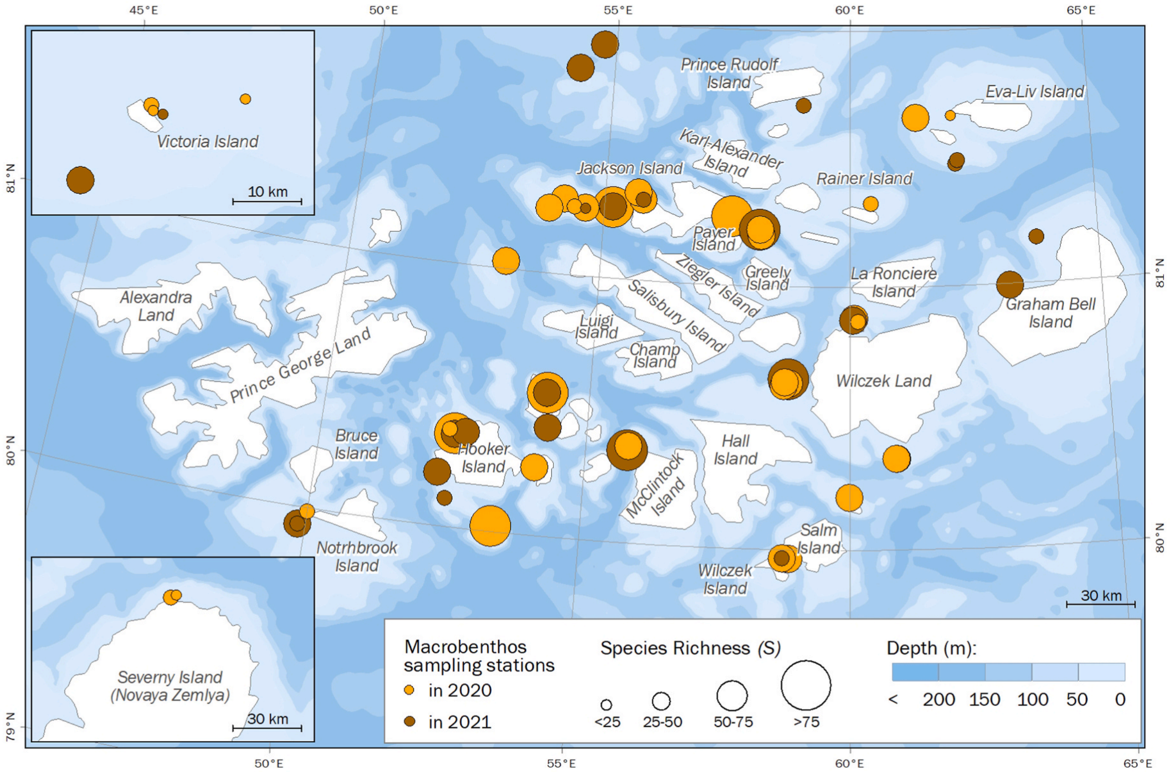

Fig. 3. Species richness (*S*) - number of taxa of macrobenthos identified at each sampling station in 2020 and 2021.

taxonomic hierarchy possible (Appendix 2).

Maps were generated using ArcMap v10.8.1. by the standard geoprocessing tools with the reference coordinate system Albers/WGS_1984.

Oceanographic data (temperature and salinity values) were interpolated using weighted-average griding method in Ocean Data View software v.5.8.0 (Schlitzer, 2024) and visualised using Adobe Illustrator Software.

3. Results

3.1. Oceanographic conditions

The near-bottom water temperatures in the western side of the research area presented sub-zero values, ranging from −0.2 to −1.3 °C. Near-bottom salinity at these stations varied from 33 to 35.2 PSU. In contrast, the eastern side featured slightly warmer temperatures, ranging from 0.1 to 1.4 °C, and similar salinity between 33.4 and 34.5 PSU. The highest values of near-bottom temperature and salinity were observed at the southernmost station south-east from Wilczek Island with measurements of 1.4 °C and 34.5 PSU respectively. The coldest near-bottom waters were found near Prince Rudolf Island, at one of the northernmost stations, where temperatures dropped to −1.3 °C and salinity was recorded at 34.15 PSU, respectively. The full vertical profiles of water column salinity and temperature of the water column were characterised by minor interannual differences. Fig. 2 presents the thermohaline characteristics recorded throughout the study area. In 2020, at the same sounding stations used in 2021, salinity values were generally lower, ranging from 33 to 34.4 PSU, and temperatures were higher, varying from −1 °C to +1.75 °C. In contrast, in 2021, salinity ranged from 33.2 to 35.5 PSU and temperatures varied from −1 °C to +1 °C at these stations. No similarity in the location of relative maxima of thermohaline characteristics of the water column was observed in 2020–2021.

The relatively low salinity values (up to 34 PSU) can be attributed to both the relatively shallow depth range of the sampling locations (11–176 m) and the influx of fresh river water and glacial melt from the islands of the archipelago. Similar conditions were also observed in the waters of the fjords of the Svalbard archipelago (Cokelet et al., 2008; Skogseth et al., 2020).

The summary of key parameters including depth, near-bottom temperature and near-bottom salinity, is presented in Table 1. The prefix in the station number corresponds to the sampling year (2020 or 2021, respectively).

3.2. Macrobenthos

A total of 143,577 specimens and 333 taxa of macrobenthic invertebrates were collected from the grab samples across the 65 sampling sites in Franz Josef Land archipelago, of which 257 were identified to species level and 44 to genus level. These included 118 Arthropoda species, 92 Mollusca species, 81 Annelida species, and 22 Echinodermata species. The remaining groups, including Brachiopoda, Bryozoa, Cnidaria, Porifera and others were presented by only a singular or a few species.

The mean species (taxa) richness was 56 ± 19 taxa per station, ranging from 8 (station 20_13) to 99 (station 21_27) (Fig. 3). The predicted total number of species according to the Chao-2 estimator was 395 ± 19 species, therefore the identified species in this paper characterise roughly 84 % of the predicted benthic biodiversity in the research area. Shannon index was 2.9 ± 0.5, corresponding to a community with many taxa mostly with few individuals each. Mean Dominance index (*D*) was 0.1 ± 0.1, indicating heterogeneous community with low dominance of any single taxa. Fig. 4 illustrates Shannon index and Dominance for each station.

The biggest contribution to mean wet biomass (g m^{-2}) was made by Mollusca (56 %) followed by Echinodermata (17 %), Annelida (10 %) and Arthropoda (10 %). The same groups but in different order dominated the species abundance (ind m^{-2}), with the biggest values represented by Annelida (55 %), followed by Echinodermata (17 %),

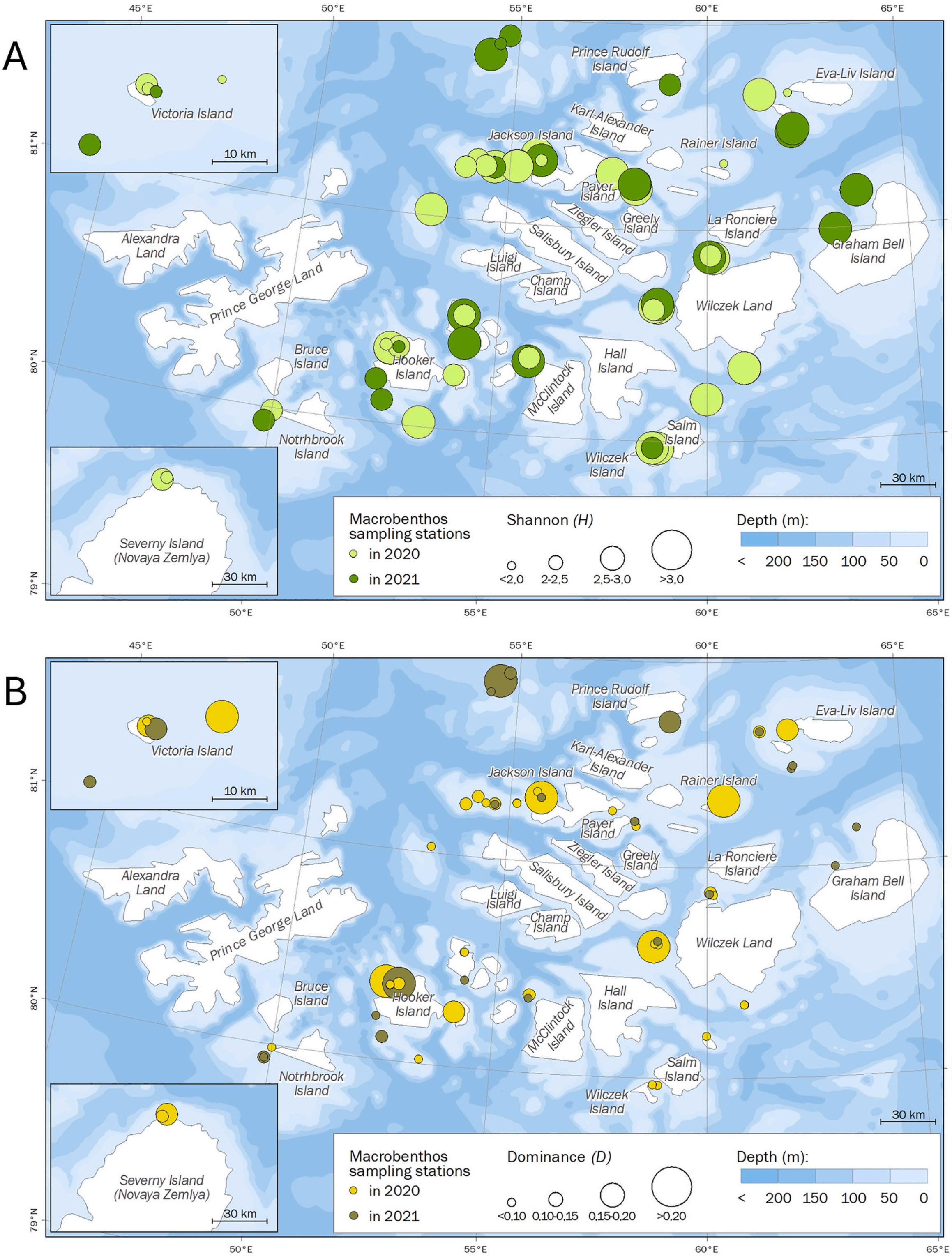

Fig. 4. Values of (A) Shannon diversity index (*H*) and (B) Dominance (*D*) index for each macrobenthic sampling station.

Mollusca (13 %), and Arthropoda (12 %) (Fig. 5).

Both biomass and abundance of macrobenthos in the research area were highly heterogeneous and varied greatly between the sampling sites. The mean abundance was 2228 ± 39 ind. m^{-2}, ranging from 156 ± 2 ind. m^{-2} (station 21_19) to 6543 ± 162 ind. m^{-2} (station 20_05). The mean biomass was 420 ± 14 g m^{-2}, ranging from 3 ± 0.1 g m^{-2} at station 21_11, to 3994 ± 151 g m^{-2} at station 21_27. The main contribution to overall biomass of macrobenthos was attributed to bivalve mollusc *Hiatella arctica*, forming 36 % of it. The values of biomass were noticeably higher than in the central and southern parts of the Barents Sea (50–150 g m^{-2}, as reviewed in Denisenko (2013)), but agree with the high biomass values previously reported around Franz Josef Land (Dahle et al., 2009). Distribution of biomass, abundance, and relative production across the sampling sites is shown on a map in Fig. 6.

The ANOSIM analysis revealed significant differences for biomass and abundance of macrobenthos between the two sampling years (2020

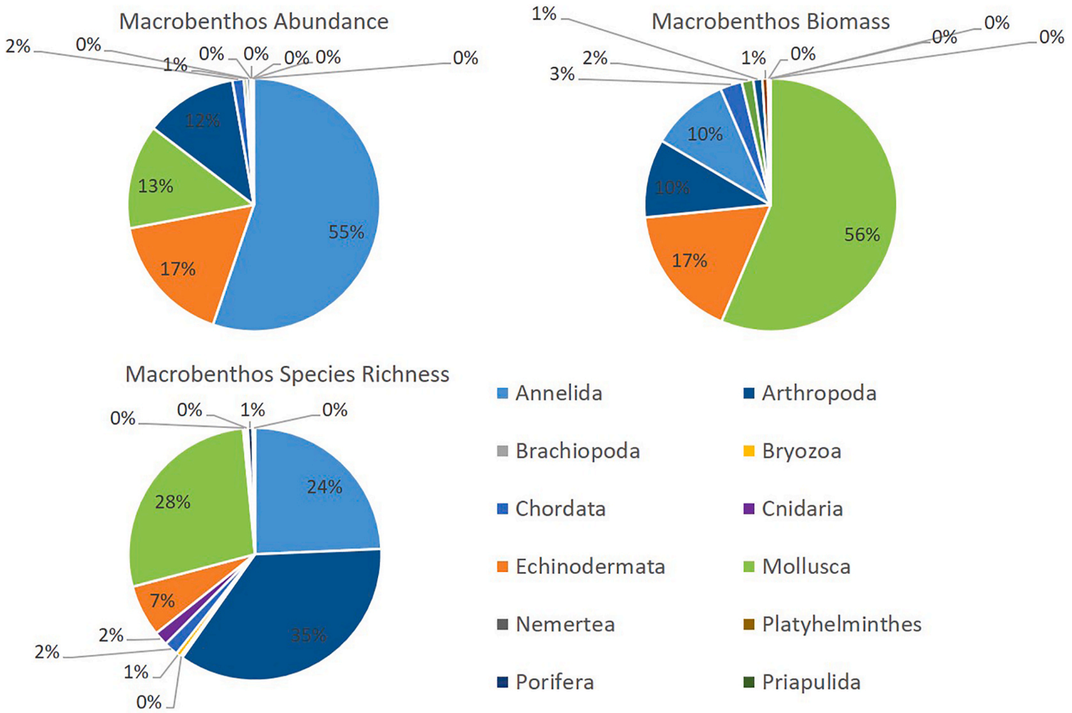

Fig. 5. Overall contributions of macrobenthic taxa to mean abundance (ind.m^{-2}), biomass (g m^{-2}) and species richness in the research area.

and 2021) (Biomass $p = 0.05$; $R = 0.04$, overall average dissimilarity 87.29; Abundance $p = 0.006$; $R = 0.08$, overall average dissimilarity 76.4). According to SIMPER, differences in biomass were mostly driven by *Hiatella arctica* (22.41 %) and *Strongylocentrotus* sp. (11.84 %); whereas differences in abundance were formed by smaller contributions from larger group of species, including *Ophiura robusta* (10.33 %), *Pholoe longa* (6.48 %), *Scoloplos armiger* (4.58 %), *Apistobranchus tullbergi* (3.82 %), *Chaetozone setosa* (3.23 %) and other species.

The near-threshold p-value (ANOSIM $p = 0.056$, $R = 0.4$) suggested that there might be a difference between macrobenthos of Franz Josef Land and Victoria Island stations and from open-water stations (ANOSIM $p = 0.056$, $R = 0.4$), characterised by low biomass (<400 g m^{-2}). No statistical difference was determined between the Novaya Zemlya and Franz Josef Land samples. In the following paragraph, we focused on the description of the benthos within the research area of Franz Josef Land.

Benthic assemblages (communities of macrobenthic species co-occurring together and characterised by species composition and affinity to certain environmental parameters) were determined by the dominant species in the relative production index. Several dominant species were identified, often co-occurring with each other. In general, three shallow-water types of macrobenthic assemblages were observed: (1) *Strongylocentrotus* sp. – *O. robusta*, (2) *H. arctica* – *O. robusta*, and (3) *Astarte* spp. To assess the differences between the assemblages, first, all stations were plotted with nMDS (using the relative production index matrix). The majority on the stations fell within a single 95 % confidence ellipse (Fig. 7A); the only outliers were remote stations from Victoria Island (20_13; 20_34; 21_05). This initial nMDS plot did not reveal distinct grouping (Fig. 7A), as intermediate forms exist between the potential communities. However, different dominant species were observed across the stations by Relative production (*P*) index, therefore 7–9 typical stations (with strongest dominance and most characteristic species) for each assemblage were selected based on dominant and subdominant species present at the station and plotted (total $n = 23$), which resulted in three clearly distinguished groups identified on nMDS plot (Fig. 7B) and supported by ANOSIM results (*Hiatella arctica*–*Ophiura robusta* VS *Astarte* spp. $p = 0.02$; *Strongylocentrotus* sp.–*Ophiura robusta* VS *Astarte* spp. $p = 0.01$; *Strongylocentrotus* sp.–*Ophiura robusta* VS *Hiatella arctica*–*Ophiura robusta* $p = 0.01$).

H. arctica contributed most to the differences between the stations according to SIMPER analysis (Table 2).

The canonical correspondence analysis (CCA) revealed minimal impact of temperature and salinity on the structure of macrobenthic communities (Appendix 3), a finding further supported by a Mantel test (Correlation R: −0.02427; $p = 0.5233$, based on 9999 permutations) that showed no significant correlation between environmental factors (Euclidean distances) and biotic data (Bray-Curtis similarity index). A tendency was observed for *S.* sp.–*O. robusta* to occupy shallower areas than *H. arctica*–*O. robusta*.

3.3. Benthic habitats

Video footage obtained at 29 benthic sampling stations was qualitatively assessed for macrofauna and characteristics of the seafloor landscapes to identify benthic habitats. A total of 34 species and higher taxa of macrobenthos were visually identified on the recordings, 11 of which were only present on video recordings (not captured by grab sampling). Full list of taxa identified on video recordings is supplied in Appendix 2.

Ophiura robusta was the dominant in sightings species in the area, spotted at 23 out of 29 studied videos. Other common forms included colonial hydroids, pycnogonids, brittle star *Ophiacantha bidentata*, and sponges, including *Alcyonidium* sp. Occasional sightings included sea urchins *Strongylocentrotus* sp., actinarians *Hormathia digitata*, gastropod molluscs *Buccinum* sp. and a predatory starfish *Crossaster papposus*.

Three types of seafloor habitats were characterised on video recordings (see Fig. 8 and 9).

1. Sea kelp (*Laminaria* sp.) on very exposed sand/bedrock, often turbulent. Stations: 20_13, 20_18, 20_33, 20_34, 20_36, 20_37, 21_19.
2. *Hiatella arctica* shells beds on muddy sand with small pebbles and occasional boulders. Often with *Lithothamnion* sp. and red seaweeds. Stations: 21_26, 21_22, 21_21, 20_27, 20_26, 21_03, 20_22, 21_06, 20_30, 21_27, 21_12.

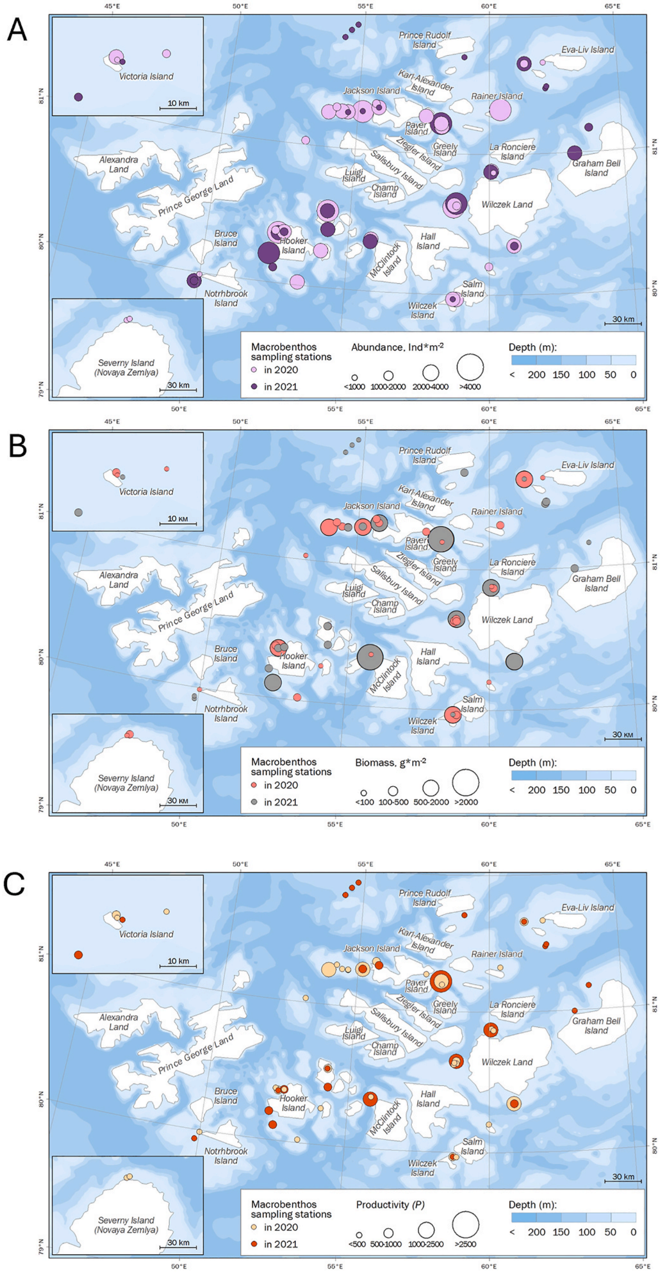

Fig. 6. Values of (A) Abundance (ind m^{-2}); (B) Biomass (g m^{-2}) and (C) Relative production (*P*) of macrobenthos at the grab sampling sites in Franz Josef Land in 2020–2021.

3. Muddy sand with shells, pebbles and occasional boulders, also often with *Lithothamnion* sp. and red seaweeds. Stations: 20_5, 20_38, 20_6, 20_31, 21_13, 20_32, 20_35, 21_11, 20_28.

Sea kelp (*Laminaria* sp.) habitat, typically found on very exposed sand or bedrock, was observed at a relatively shallow average depth range of 22.3 ± 2.9 m. In contrast, habitat type two, characterised by *Hiatella arctica* shell beds on muddy sand mixed with small pebbles and occasional boulders, was found at deeper sites averaging 40.5 ± 3.8 m. The third habitat type, consisting of muddy sand with shells, pebbles, and occasional boulders, had an average depth of 42.2 ± 5.5 m. The distribution of benthic habitats exhibited high heterogeneity with abrupt changes in a relatively small area; for instance, a visible border between Type 1 and Type 2 seabed areas was observed at station 21_24 (Fig. 8D–E).

Approximate correspondence of these habitats with EUNIS habitat types (EUNIS, 2022) and correspondence to communities of macrobenthos based on grab sampling is summarised in Appendix 4.

4. Discussion

4.1. Biomass of macrobenthos in Franz Josef Land

In this study, the benthic fauna of the Barents Sea region around Franz Josef Land were found to exhibit unusually high biomass and relatively high biodiversity when compared to other areas of the Barents Sea (Denisenko, 2013). Dahle et al. (2009) reported the highest previously documented biomass within the 51–100 m depth range near Franz Josef Land at 2146 g m^{-2}, the highest among comparative data from the Eurasian Arctic Shelf, Lara Sea, Svalbard, northwestern Barents Sea, and the Pechora Sea. Our findings significantly surpass these, with a maximum value at station 21_27 (62 m depth) reaching 3994.27 g m^{-2}. The mean biomass of 420.6 g m^{-2} in this study aligns with other high biomass regions like Svalbard and NW Novaya Zemlya (Kulakov et al., 2004; Dahle et al., 2009; Denisenko, 2013). Importantly, this study also shows highly heterogenous distribution of macrobenthos with stations with high biomass neighbouring low biomass areas, which also corresponds with literature (Frolova et al., 2014; Dvoretsky and Dvoretsky, 2024).

Across the pan-Arctic scale, the benthic biomass from Franz Josef Land is comparable to that observed in the Bering and Beaufort Seas, and exceeds values recorded elsewhere (Table 3). The absolute maximum values were reported from the Chukchi Sea (Grebmeier and Cooper, 2014), attributed to the northward inflow of nutrient-rich, warmer Pacific waters through the Bering Strait, creating a productive frontal zone (Grebmeier et al., 2006). Benthic biomass generally decreases from shelf areas toward abyssal depths due to reduced food supply, with exceptionally low values reported from the notoriously understudied Central Arctic Ocean (<1 g m^{-2}, wet mass), except for a recorded maximum of 650 g m^{-2} at 508 m depth at a station in the Central Arctic Ocean northwest of Franz Josef Land (N 82.123333; Vedenin et al., 2018).

Comparing benthic biomass across different studies poses challenges due to the varied methodologies employed in biomass assessment, including different mesh sizes and the lack of standard definitions of the size classes included in the measurements. While many studies report ash-free dry weight (AFDW) or carbon content, others may use wet biomass. The recent publication by Lebrun (2023) offers a comprehensive review and compilation of Arctic benthic species data, enhancing understanding of both abundance and biomass measurements, including wet biomass calculations. To facilitate more accurate comparisons and better contextualise findings within the regional framework moving forward, it is recommended that future studies in Franz Josef Land adopt AFDW measurements.

4.2. Macrobenthic assemblages

This study found similar species compositions between Franz Josef Land and northwestern Novaya Zemlya, with dominant species including *Hiatella arctica*, *Astarte* spp., *Ophiopleura borealis* and *Golfingia* sp. Statistical analyses revealed no significant differences between samples from Novaya Zemlya and Franz Josef Land.

Bivalve molluscs *Hiatella arctica* and *Astarte elliptica* dominated the macrobenthic biomass in Franz Josef Land according to Dahle et al. (2009), which agreed with the results of this study. Other high-density species include *Ophiura robusta, Balanus balanus, Strongylocentrotus pallidus*, and in shallows – *Pholoe synopthalmica, Aricidea hartmanni, Ophiocten sericeum, Chone* sp. (Dahle et al., 2009) which were also found in this research. UPGMA clustering analysis using the Bray-Curtis similarity index exhibited 40–50 % similarity across most stations, indicating significant variability, consistent with previous studies (Dahle et al., 2009; Frolova et al., 2014; Dvoretsky and Dvoretsky, 2024).

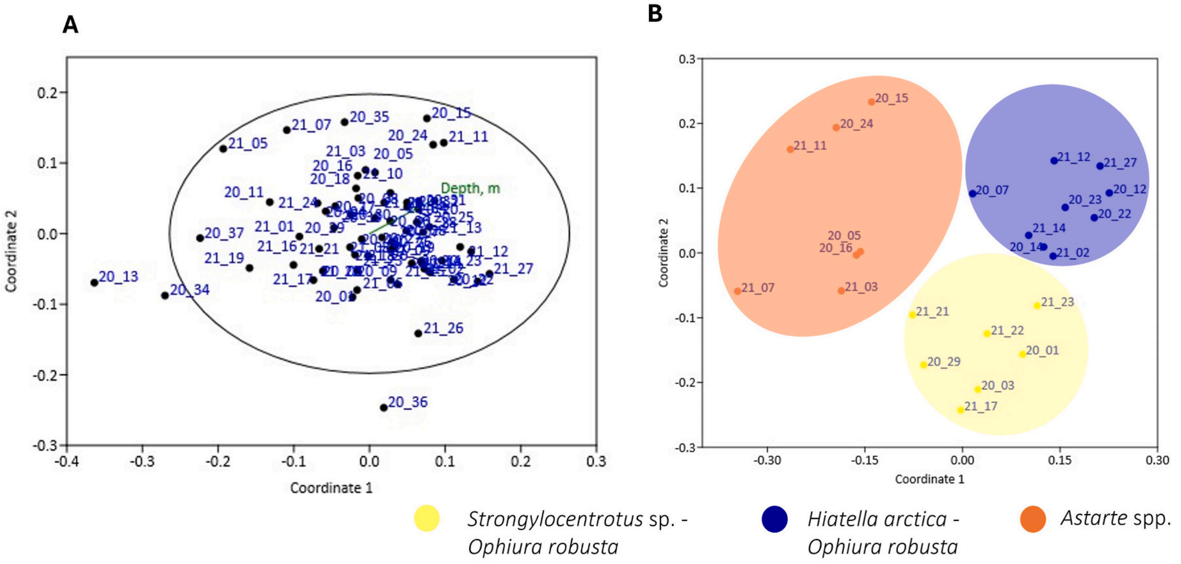

Fig. 7. Groups of stations based on nMDS plotting based on the Bray-Curtis similarity index for the relative production values (A) All stations plotted by nMDS with a depth factor plotted – no groups or effects of depth observed, the majority on the stations fell within the one 95 % confidence ellipse; (B) Only typical stations for each community selected (n = 23), 3 assemblages are distinguished: (1) *Strongylocentrotus* sp. – *Ophiura robusta* (yellow); (2) *Hiatella arctica* – *Ophiura robusta* (blue); and (3) *Astarte* spp. (orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Species contribution to dissimilarity between benthic assemblages produced by SIMPER analysis (only taxa with >1 % contribution shown). Calculated for mean values of Relative production (*P*) index. Species contributing >5 % to overall dissimilarity included.

Taxon	Average dissimilation	Contribution %	Cumulative %	St–Oph*	Hi–Oph**	Ast***
Hiatella arctica	28.27	31.06	31.06	7.04	590	0.0859
Strongylocentrotus sp.	9.09	9.987	41.05	46.8	80.8	0
Balanus balanus	7.601	8.351	49.4	0	154	0
Artacama proboscidea	6.688	7.348	56.75	1.83	119	5.17
Astarte montagui	5.545	6.093	62.84	2.8	14	43.5

Communities: *St–Oph – *Strongylocentrotus* sp. – *Ophiura robusta,* ** – *Hiatella arctica* – *Ophiura robusta*, and *** – *Astarte* spp.

The high macrobenthic heterogeneity might stem from the mosaic distribution of species with varying ecological traits. Environmental factors such as substrate type, depth, currents and POC flux could further influence macrobenthic distribution. Statistical identification of specific assemblages may not always be feasible; however, within a subset of Franz Josef Land stations classified by dominant macrobenthos (n = 23) in this study, nMDS analysis segregates three distinct groups, confirmed by ANOSIM.

Strongylocentrotus sp. and *H. arctica* show overlapping distributions in some stations (n = 7) but *Strongylocentrotus* sp. favours greater depths and is typically found below 70 m. The biomass of the two assemblages was also notably different with 800 ± 200 g m^{-2} for stations with *H. arctica*, and 260 ± 80 g m^{-2} for stations with *Strongylocentrotus* sp. The remaining stations in the research area were characterised by either shallow-water (<50 m) assemblage of bivalve molluscs *Astarte* spp. with a relatively high biomass (230 ± 70 g m^{-2}), or poly-dominant group with the lowest biomass. The brittle star *O. robusta* formed a significant contribution to macrobenthic biomass and abundance at 32 stations and was associated with both *H. arctica* and *Strongylocentrotus* sp. Overall, macrobenthos of the research area can be characterised as one heterogeneous community, dominated by *H. arctica, Strongylocentrotus* sp. and *O. robusta*, with three variations, showing regional similarities with other parts of the Barents Sea, such as Vaigach Island in the Pechora Sea, where communities also display high variability and multiple assemblage structures (Gebruk et al., 2021b; Denisenko et al., 2019).

4.3. Benthic habitats and limitations of video analysis

The ROV video footage obtained in the present study was used to assess the research area for macrofauna. The lists of species identified from ROV footage and grab samples significantly overlap, with approximately 32 % of species unique to ROV video recordings. Several mobile and large sessile animals were captured by ROV only (Appendix 2). Typically, grab samples allow a better assessment of infauna, whilst ROV recordings capture mobile migratory species often underrepresented in grab samples. ROV footage also allows to assess areas with hard substrates, such as the exposed bedrock, which are unsuitable for grab sampling.

An additional valuable insight derived from the video footage is the visual assessment of habitats, their distribution, and overlap, beyond just compiling species lists. In this study, three habitat types were delineated (Fig. 8), which further elucidates the observed variability in macrobenthos distribution.

Appendix 2 compiles data from grab sampling and video recordings, encompassing dominant macrobenthic fauna, benthic assemblages, observed macrofauna, and habitat classifications. The comparison illustrates that the distribution of benthic habitats identified from the video analysis did not always correspond to the macrobenthic communities identified at the corresponding stations from grab samples. For instance.

- Type 1 habitat (*Hiatella arctica* shells beds on muddy sand with small pebbles and occasional boulders, corresponding to EUNIS Habitat

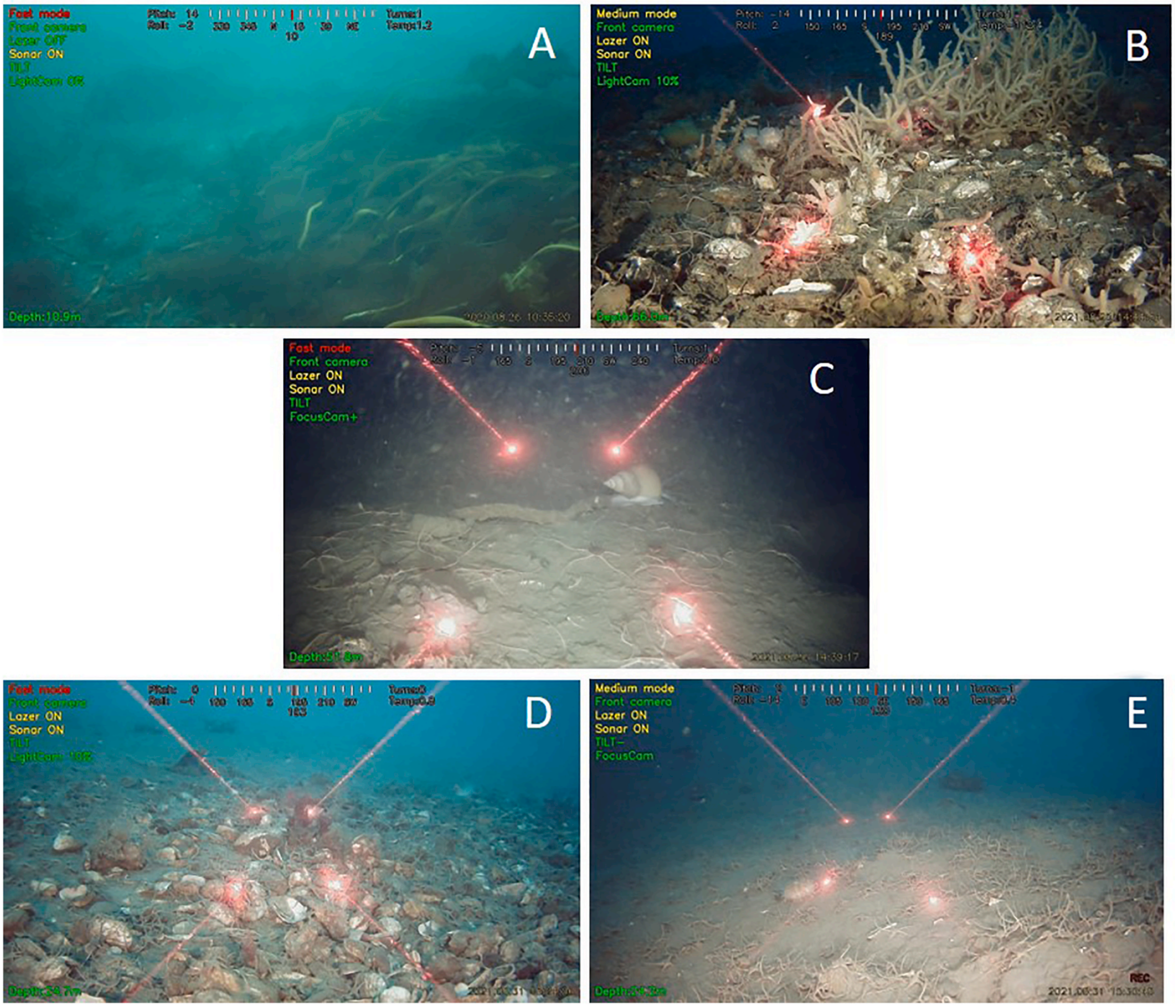

Fig. 8. Different types of seafloor habitats: (A) Station 201_13 – Sea kelp (*Laminaria* sp.) on very exposed sand/bedrock, often turbulent. (B) Station 21_12 – *Hiatella arctica* shells beds on muddy sand with small pebbles and occasional boulders. Often with *Lithothamnion* sp. and red seaweeds. (C) Station 21_13 – Muddy sand with shells, pebbles and occasional boulders, also often with *Lithothamnion* sp. and red seaweeds. (D–E) Station 21_24 represents a transitional landscape, both screen grabs are taken from the same station within a few metres between each other but correspond to different habitats – (D) corresponds to *Hiatella arctica* shells beds on muddy sand with small pebbles and occasional boulders, and (E) corresponds to muddy sand with shells, pebbles and occasional boulders. Laser pointers are spaced 10 cm apart. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

A5.13) in the research area also includes the *Strongylocentrotus* sp., which is a dominant species for another macrobenthic cluster

- *Hiatella arctica* is prevalent throughout the research area, often dominating in both Type 1 and Type 2 habitats
- The macrobenthic community dominated by *Astarte* spp. is present in some stations which belong to both Type 1 and Type 2 habitats.

ROV video recordings provide georeferenced imagery data and are a non-destructive means for benthic assessments, increasingly favoured for their minimal environmental impact (López-Garrido et al., 2020). However, several challenges were identified in this study: reduced visibility due to turbidity or poor lighting, the risk of double-counting organisms, difficulty in taxonomic identification when morphological features are unclear, and challenges in assessing population size structures without size references in the footage. To enhance the quality of ROV video data for quantitative assessments, it is crucial to standardise protocols. Key measures include using parallel laser pointers set at a known distance to estimate the size of organisms and their distance from the seafloor, as well as ensuring consistent camera tilt, speed, direction, and distance from the seafloor (Mokievsky, 2019)

4.4. *Characteristics of Franz Josef Land benthic ecosystems*

Seafloor sediments in the research area were heterogeneous and included inequigranular sand, silty clay, shell sand with gravel and stones, and mixed sediment types. No trends or patterns were observed with regards to the distribution of macrobenthic assemblages and types of sediments, with both *H. arctica* and *Strongylocentrotus* sp. found in silt, sand, and gravel. Distribution of benthic communities was characterised by high spatial heterogeneity. Minor role of the granulometric type of sediments in distribution of macrobenthos was previously noted for Franz Josef Land, with total organic carbon in sediments being more important than the grain size (Dahle et al., 2009).

Notably, the high biomass of macrobenthos in the area attracts benthic predators, including Atlantic walruses (*Odobenus rosmarus*), which are known to migrate between Svalbard and Franz Josef Land, likely using Franz Josef Land as summer feeding grounds (Wiig et al., 1996; Freitas et al., 2009; Gavrilo and Martynova, 2017). Macrobenthic species that contribute most to biomass in the research area, namely *Hiatella arctica*, are known to form the bulk of walrus diet in other regions, e.g., in the Greenland Sea (Born et al., 2003). Therefore, foraging activity of benthic predators could potentially be an additional important factor driving macrobenthic biomass and distribution and

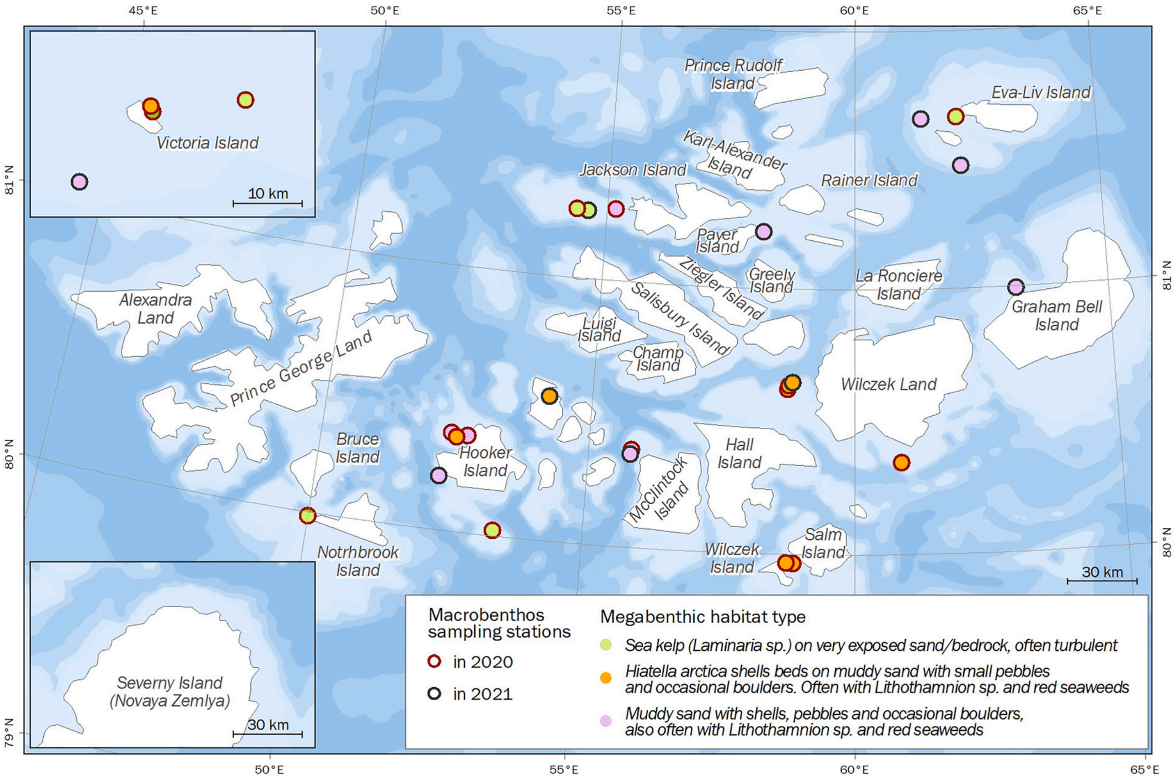

Fig. 9. Different types of seafloor habitats identified from video data: (1) Green circle – Sea kelp (*Laminaria* sp.) on very exposed sand/bedrock, often turbulent. (2) Orange circle – *Hiatella arctica* shells beds on muddy sand with small pebbles and occasional boulders. Often with *Lithothamnion* sp. and red seaweeds. (3) Purple circle – Muddy sand with shells, pebbles and occasional boulders, also often with *Lithothamnion* sp. and red seaweeds. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Maximum wet biomass values recorded in literature for macrobenthos in different areas of the Arctic.

Maximum Wet Biomass, g m^{-2}	Depth, m	Location	Reference	Size classes included in the measurements
7024.27	129	Chukchi Sea	Grebmeier and Cooper (2014)	>1 mm
3994.27	62	Franz Josef Land	This study	>0.5 mm
3222.18	49	Bering Sea	Grebmeier and Cooper (2014)	>1 mm
3131.92	57	Beaufort Sea	Grebmeier and Cooper (2014)	>1 mm
1975.22	5	White Sea	Denisenko (2009)	>1 mm
1499.81	30	Kongsfjorden, Svalbard	Voronkov et al. (2013)	>1 mm
800	70	Kara Sea (Novaya Zemlya)	Galkin et al. (2010)	>0.5 mm
650.53	508	Central Arctic Ocean	Vedenin et al. (2018)	>0.5 mm

contributing to high heterogeneity of macrobenthos. A similar hypothesis was suggested for another important feeding ground of walruses in the Pechora Sea (Denisenko et al., 2019; Semenova et al., 2019; Gebruk et al., 2021b), however, long-term monitoring of both macrobenthos and walrus population is needed to better understand this relationship and detect changes in benthic ecosystems.

High biomass of macrobenthos in Franz Josef Land was previously reported (Dahle et al., 2009), although the results of this study demonstrate even higher values in the shallow waters. Some factors that could have historically contributed to the development of this benthic biomass hot spot in the high Arctic, could include.

1. Very long coastline with complicated topography of sounds, fjords, and inter-island channels leading to elevated runoff of terrigenous organic carbon (Govorukha, 1968). High carbon stock has been previously shown for the soil cover of some islands of Franz Josef Land (Nikitin et al., 2020). The oceanographic profiles of the stations in the central part of the archipelago clearly show the decreased salinity, which is also likely linked to the influence of the terrestrial runoff.

Similarly high values of benthic biomass (up to 4 kg m^{-2}) were reported in the northwestern Sakhalin in the North Pacific, which was largely influenced by the rich in organic carbon riverine input from the Amur River, combined with the hydrographic conditions leading to water mixing in the near-shore lagoons and local peaks of pelagic and benthic productivity (Labai et al., 2019). Notably, the area also attracts benthic predators and is an important foraging ground of the grey whales (Labai et al., 2019).

2. Active hydrodynamic conditions of the archipelago, that are assured by the mixing of water masses of the Barents Sea origin, cold Arctic waters, and warm Atlantic waters, with an additional influence of the terrestrial runoff with reduced salinity (Govorukha, 1968). Shallow water depth around the archipelago combined with complicated topography and high compartmentation lead to strong turbulent mixing of the water column (Govorukha, 1968), which is known to positively influence productivity of plankton communities (Petersen et al., 1998).

3. An abundance of hard substrates at the depth range of up to 80 m, which might be linked to the annual ice scour from icebergs (Dahle et al., 2009). A combination of hard and soft substrates creates a variety of habitats for macrobenthos, supporting larvae settlement and biofouling. It is often shown that hard substrates are associated with much higher benthic biodiversity than soft substrates, sometimes orders of magnitude higher (Cardone et al., 2014; Gerovasileiou et al., 2017).

5. Conclusions

Overall, the macrobenthos of Franz Josef Land's shallow waters exhibit high biodiversity (333 taxa (257 species) identified in this study), characterised by species typical of the Barents Sea. Notably, it has recorded some of the highest values of wet macrobenthic biomass on the Eurasian Arctic shelf—up to 4 kg m^{-2} at specific locations (e.g., station 27_21). These results suggest that current estimates of benthic standing stock may be conservative, indicating that the carbon sequestration potential of the Eurasian Arctic shelf could be more significant than previously estimated. Notably, macrobenthic biomass in the study area had highly heterogeneous spatial distribution with high-biomass stations neighbouring low-biomass values. The largest contribution to benthic biomass was formed by macrobenthic invertebrates that are known as foraging items for the Atlantic walruses, which are actively using the archipelago as feeding grounds (Solovyova et al., 2024) – namely, bivalve molluscs *Hiatella arctica* and *Astarte* spp. The ROV video recordings revealed three overlapping types of benthic habitats in the area. Notably, the benthic habitats identified from the video analysis did not always correspond to the macrobenthic communities identified at the corresponding stations from grab samples. It is recommended to establish long-term monitoring to assess temporal variability of these diverse and productive benthic ecosystems in the context of ongoing climate change and foraging pressure from benthic feeders.

CRediT authorship contribution statement

Anna Gebruk: Writing – original draft, Project administration, Formal analysis, Conceptualization. **Alexander Kokorin:** Formal analysis, Data curation, Conceptualization. **Maria Mardashova:** Formal analysis, Data curation. **Yulia Ermilova:** Visualization, Formal analysis. **Victoria Melnikova:** Writing – original draft, Methodology, Investigation. **Ilya Fedorov:** Writing – original draft, Methodology, Data curation. **Alexandra Barymova:** Methodology, Data curation. **Olga Konovalova:** Project administration, Conceptualization. **Vladimir Rogozhin:** Writing – review & editing, Visualization, Formal analysis. **Nikolay Shabalin:** Validation, Supervision, Conceptualization. **Svetlana Artemyeva:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Viatcheslav V. Rozhnov:** Writing – review & editing, Validation, Supervision. **Artem Isachenko:** Validation, Supervision. **Renata Lazareva:** Validation, Supervision. **Vadim Mokievsky:** Writing – original draft, Formal analysis, Conceptualization.

Data availability

Data used in this article are available online in a findable, accessible, interoperable and reusable (FAIR) data repository PANGAEA (Gebruk et al., 2024; Kokorin et al., 2024a, 2024b).

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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Appendices.

Appendix 1

List of sampling stations with coordinates, dates of sampling and depth.

Site	N	E	Sampling Date	Depth, m
20_01	77.03186167	67.80372333	21/08/2020	35
20_03	77.02602833	67.706455	21/08/2020	23
20_04	80.19872	59.98416833	23/08/2020	35
20_05	80.61891667	58.71873333	24/08/2020	18
20_06	80.63376167	58.733205	24/08/2020	22
20_07	80.64381667	58.805475	24/08/2020	27
20_08	80.62919167	58.82254333	24/08/2020	45
20_09	80.86570167	60.15205333	August 25, 2020	40
20_10	80.877845	60.07828833	25/08/2020	32
20_11	81.19308667	58.21064	25/08/2020	51
20_12	81.21651333	58.18092333	25/08/2020	18
20_13	81.66253167	62.09655333	26/08/2020	23
20_14	81.65618667	61.36952167	26/08/2020	11
20_15	81.32176667	60.4179	27/09/2020	33
20_16	81.26481	57.601375	27/09/2020	21
20_17	81.26308833	54.62398167	27/09/2020	30

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(*continued*)

Site	N	E	Sampling Date	Depth, m
20_18	81.26556833	54.39414	28/08/2020	23
20_19	81.29167333	54.18970833	28/08/2020	26
20_20	81.31233333	55.78796667	29/08/2020	32
20_21	81.33777667	55.67423333	29/08/2020	28
20_22	81.27584667	55.17532167	29/08/2020	32
20_23	81.250965	53.89932667	30/08/2020	37
20_24	81.02986667	53.14055	30/08/2020	49
20_25	80.54351167	54.19668167	30/08/2020	176
20_26	80.36400333	52.72884667	30/08/2020	49
20_27	80.36930333	52.42329167	31/08/2020	35
20_28	80.35356	52.52526333	31/08/2020	41
20_29	80.25858333	54.08108333	01/09/2020	71
20_30	80.36733	55.812265	01/09/2020	36
20_31	80.34505	60.87500833	03/09/2020	37
20_32	79.96729333	58.86829167	03/09/2020	31
20_33	80.021675	53.36647	03/09/2020	50
20_34	80.16658333	36.75715	05/09/2020	25
20_35	80.17260167	36.73455333	05/09/2020	14
20_36	80.223015	37.28641167	05/09/2020	51
20_37	79.98725667	50.00219167	06/09/2020	25
20_38	79.96712833	58.74137833	08/09/2020	17
21_01	79.96712833	58.73971167	20/08/2021	32
21_02	80.10737	52.47343	21/08/2021	33.5
21_03	80.20275	52.28246667	21/08/2021	75
21_04	80.35307333	52.529445	21/08/2021	21
21_05	80.16635	36.8234	22/08/2021	49
21_06	80.04833333	36.48668333	23/08/2021	45
21_07	79.93446667	49.85821667	23/08/2021	54
21_08	79.934145	49.86128	23/08/2021	34.5
21_09	80.36354667	52.72934167	24/08/2021	40
21_10	80.41073333	54.25518333	24/08/2021	44.5
21_11	80.54378333	54.19346667	25/08/2021	64
21_12	80.34885833	55.79208167	25/08/2021	50
21_13	80.64451667	58.8114	26/08/2021	26
21_14	81.31245	55.78345	27/08/2021	39
21_15	81.27742333	55.17967667	28/08/2021	65
21_16	81.90855	54.749	28/08/2021	67
21_17	81.86573333	54.50176667	28/08/2021	76
21_18	81.80671667	54.27135	28/08/2021	21.5
21_19	81.26191167	54.62456833	29/08/2021	26.5
21_20	81.70395	59.01945	29/08/2021	32
21_21	81.65623333	61.36825	30/08/2021	25.5
21_22	81.47111667	62.16265	30/08/2021	27.5
21_23	81.48628333	62.21181667	31/08/2021	25.5
21_24	81.17378333	63.75208333	31/08/2021	24.7
21_25	80.99396667	63.17185	31/08/2021	26.5
21_26	80.87123333	60.06061667	01/09/2021	63.5
21_27	81.2168	58.17411667	01/09/2021	31
21_28	80.34505	60.88096667	02/09/2021	17

Appendix 2

List of taxa of benthic invertebrates observed on ROV video recordings.

Phylum	Species	No. of stations observed	Presence in grab samples
Annelida	*Harmothoe fragilis*	1	+
Annelida	Polychaeta sedentaria indet.	3	+
Arthropoda	*Balanus* sp.	5	+
Arthropoda	Caprellidae Gen.sp.indet.	3	+
Arthropoda	Pantopoda Gen.sp.indet.	6	+
Arthropoda	*Sclerocrangon boreas*	4	
Bryozoa	*Alcyonidium disciforme*	2	+
Bryozoa	*Alcyonidium gelatinosum*	7	+
Bryozoa	Bryozoa Gen.sp.indet.	11	+
Cnidaria	*Cerianthus lloydii*	5	+
Cnidaria	*Corymorpha glacialis*	6	
Cnidaria	*Gersemia rubiformis*	5	
Cnidaria	*Halcampa arctica*	1	
Cnidaria	*Hormathia digitata*	8	
Cnidaria	Hydrozoa Gen.sp.indet.	16	+
Cnidaria	*Liponema multicorne*	1	

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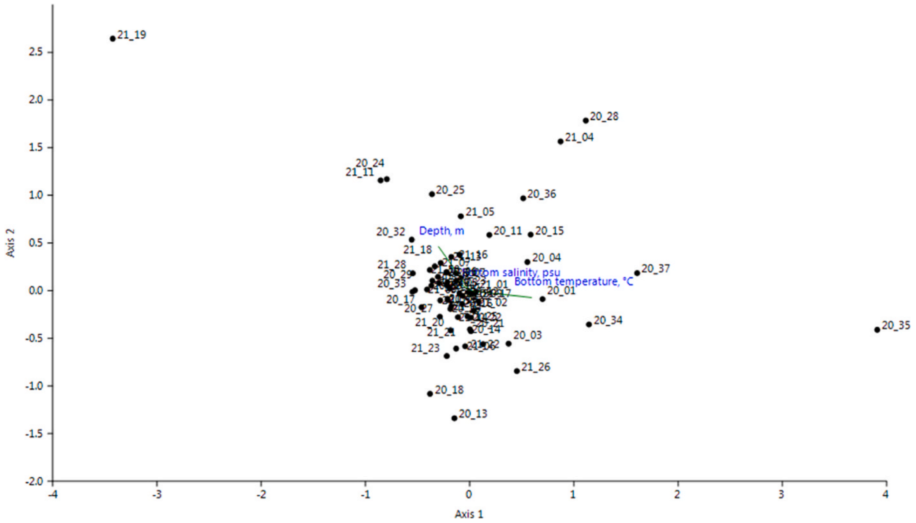
(*continued*)

Phylum	Species	No. of stations observed	Presence in grab samples
Cnidaria	*Stomphia coccinea*	4	
Echinodermata	*Crossaster papposus*	6	+
Echinodermata	*Gorgonocephalus arcticus*	1	
Echinodermata	*Heliometra glacialis*	2	
Echinodermata	*Ophiacantha bidentata*	12	+
Echinodermata	*Ophiura robusta*	23	+
Echinodermata	*Solaster syrtensis*	1	
Echinodermata	*Strongylocentrotus* sp.	8	+
Mollusca	*Buccinum* sp.	7	+
Mollusca	*Cryptonatica affinis*	1	+
Mollusca	*Dendronotus elegans*	2	
Mollusca	*Hiatella arctica*	4	+
Mollusca	*Serripes groenlandicus*	2	+
Mollusca	*Tonicella marmorea*	1	+
Nemertea	Nemertea Gen.sp.indet.	2	+
Plathelminthes	Plathelminthes Gen.sp.indet.	1	+
Porifera	Porifera Gen.sp.indet.	6	+
Tunicata	Tunicata Gen.sp.indet.	2	+
Ochrophyta	*Laminaria* sp.	8	+
Rhodophyta	*Lithothamnion* sp.	7	+
Rhodophyta	Rhodophyta Gen.sp.indet.	8	+

Appendix 3

Canonical Correspondence Analysis (CCA) Biplot for Macrobenthic Communities. The graph illustrates the relationship between macrobenthic assemblages and environmental parameters (temperature, salinity, and depth) across various sampling stations. Arrows represent the direction and magnitude of environmental factors influencing species distribution.



Appendix 4

Correspondence of dominant benthic species with macrobenthic assemblages identified from grab sampling for each sampling site. Substrate type, depth and habitat classification also listed for each video transect.

Station	Depth, m (CTD)	Macrobenthic assemblage	Dominant macrobenthos species (by biomass from grab samples)	Macrofauna and macrophytes observed on ROV	Substrate type	EUNIS habitat type	Habitat characterisation
20_22	37	*Hiatella arctica*	*Artacama proboscidea*, *Balanus balanus*, *Hiatella arctica*	*Balanus* sp., *Strongylocentrotus* sp.	silty sand with gravel	A5.13: Infralittoral coarse sediment	*Hiatella arctica* shells beds on muddy sand with small pebbles and occasional boulders. Often with *Lithothamnion* sp. and red seaweeds
20_26	35	transitional	*Artacama proboscidea*, *Hiatella arctica*, *Ophiura robusta*, *Strongylocentrotus* sp.	*Ophiura robusta*, *Strongylocentrotus* sp., red seaweeds *Lithothamnion* sp.	inequigranular sand with gravel		

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(*continued*)

Station	Depth, m (CTD)	Macrobenthic assemblage	Dominant macrobenthos species (by biomass from grab samples)	Macrofauna and macrophytes observed on ROV	Substrate type	EUNIS habitat type	Habitat characterisation
20_27	41	transitional	*Ophiura robusta*, *Hiatella arctica*, *Artacama proboscidea*	*Ophiura robusta*, *Strongylocentrotus* sp., *Crossaster papposus*, *Hormathia digitata*, red seaweeds *Lithothamnion* sp.	inequigranular sand with gravel and shells		
20_30	37	transitional	*Ophiura robusta*	*Ophiura robusta*, *Hormathia digitata*	inequigranular sand		
21_03	33.5	*Astarte* sp.	*Astarte borealis*, *Astarte montagui*	*Corymorpha glacialis*, *Ophiura robusta*, *Ophiacantha bidentata*, *Strongylocentrotus* sp.	fine sand with silt		
21_06	49.3	transitional	*Artacama proboscidea*, *Musculus discors*, *Strongylocentrotus* sp.	Bryozoa Gen. sp. indet.	gravelly sediments		
21_12	63.3	*Hiatella arctica*	*Hiatella arctica*	*Ophiura robusta*, *Alcyonidium gelatinosum*	silty clay		
21_21	31.8	*Strongylocentrotus* sp.	*Artacama proboscidea*, *Strongylocentrotus* sp.	*Lithothamnion* sp., *Strongylocentrotus* sp., *Hiatella arctica*, *Crossaster papposus*, *Ophiura robusta*	clayey silt with sand and gravel		
21_22	28	*Strongylocentrotus* sp.	*Strongylocentrotus* sp.	*Strongylocentrotus* sp., *Gersemia rubiformis*, *Ophiura robusta*	clayey silt with gravel		
21_26	27.4	transitional	*Strongylocentrotus* sp.	*Lithothamnion* sp., *Strongylocentrotus* sp., *Hiatella arctica*, *Crossaster papposus*, *Ophiura robusta*	silty sand with coarse sand		
21_27	62.9	*Hiatella arctica*	*Hiatella arctica*	*Lithothamnion* sp., *Alcyonidium gelatinosum*, *Heliometra glacialis*	clayey silt with shells		
20_05	22	*Astarte* sp.	*Astarte montagui*	*Ophiura robusta*, *Ophiacantha bidentata*, *Serripes groenlandicus*, *Hormathia digitata*	clayey silt with sand	A5.24: Infralittoral muddy sand	Muddy sand with shells, pebbles and occasional boulders, also often with *Lithothamnion* sp. and red seaweeds
20_06	27	transitional	*Hiatella arctica*, *Astarte montagui*, *Ophiura robusta*	*Ophiura robusta*, *Ophiacantha bidentata*, Hydrozoa Gen. sp. indet.	clayey silt with coarse sand		
20_28	71	transitional	Porifera Gen. sp., *Hiatella arctica*	*Ophiura robusta*, Porifera Gen. sp., *Gersemia rubiformis*	sandy silt		
20_31	31	transitional	*Astarte montagui*, *Musculus discors*, *Hiatella arctica*, *Astarte borealis*	*Ophiura robusta*, Porifera Gen. sp. indet., *Gersemia rubiformis*	silty sand with gravel		
20_32	50	transitional	*Hiatella arctica*, *Astarte crenata*	*Ophiura robusta*, *Ophiacantha bidentata*, Bryozoa Gen. sp. indet.	silty clay with sand		
20_35	51	transitional	*Alcyonidium disciform*, *Myriotrochus rinkii*, *Ophiura robusta*	*Ophiura robusta*, *Alcyonidium disciform*	fine sand		
20_38	25	transitional	*Astarte montagui*, *Hiatella arctica*	*Ophiura robusta*, Hydrozoa Gen. sp. indet.	silty sand		
21_11	54	*Astarte* sp.	*Astarte crenata*, *Astarte elliptica*	*Ophiura robusta*	clayey silt with very fine sand		
21_13	49.1	transitional	*Hiatella arctica*	*Ophiura robusta*, *Balanus* sp.	clayey silt with sand and gravel		
20_13	11	transitional	Gastropoda Gen. sp.	Sea kelp (*Laminaria* sp.), no macrobenthos	no data obtained	A5.52: Kelp and seaweed communities on sublittoral sediment	Sea kelp (*Laminaria* sp.) on very exposed sand/bedrock, often turbulent
20_18	26	transitional	*Pelonaia corrugata*, *Ophiura robusta*	Sea kelp (*Laminaria* sp.), no macrobenthos	no data obtained		
20_33	25	transitional	*Ophiura robusta*	Sea kelp (*Laminaria* sp.), red seaweeds *Lithothamnion* sp., *Ophiura robusta*	inequigranular sand with gravel		
20_34	14	transitional	*Harmothoe fragilis*	Sea kelp (*Laminaria* sp.), no macrobenthos	gravel with inequigranular sand		
20_36	25	transitional	*Musculus discors*	Sea kelp (*Laminaria* sp.), no macrobenthos	coarse sand with shells and gravel		
20_37	34	transitional	Molgulidae Gen. sp.	Sea kelp (*Laminaria* sp.), no macrobenthos	shells with inequigranular sand		
21_19	21.2	transitional	*Ocnus glacialis*	Sea kelp (*Laminaria* sp.), *Ophiura robusta*, *Hiatella arctica*	inequigranular sand with gravel		

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