Assessing the status, variability, and biodiversity conservation issues of Arctic benthic ecosystems of the Pechora Sea for improved management

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Abstract

The biodiversity of the Arctic Ocean is described by the Arctic Council as an "*irreplaceable cultural, scientific, ecological, economic and spiritual asset*". Global climate change together with industrial development pose major threats to Arctic ecosystems and biodiversity including but not limited to rise in water and air temperatures, loss of sea ice habitats, introduction of non-indigenous species (NIS) and anthropogenic pollution. The urgent need to protect Arctic marine ecosystems and biodiversity is emphasised in many national and international strategies and policy framework documents. Furthermore, improvement of baseline knowledge and implementation of ecosystem-based management are identified as key "*actions for biodiversity*".

Macrobenthic communities are one of the most conservative biotic components of marine ecosystems and are therefore prominently used in ecological monitoring as indicators of good environmental status of ecosystems. At the same time, macrobenthic invertebrates are focal ecosystem components as they provide food resources to sustain benthic predators of higher trophic levels. Our knowledge of Arctic benthic ecosystems, their biodiversity, temporal variability, individual and cumulative impacts of environmental stressors remain fragmentary and often insufficient for knowledge-based decision-making. This thesis aimed to improve regional knowledge through assessing the status, variability and biodiversity conservation issues of Arctic benthic ecosystems of the ecologically significant area of the Barents Sea, the Pechora Sea, for improved management.

An extensive dataset on macrobenthos of the Pechora Sea was compiled through participating in a series of expeditions to the Pechora Sea with additional samples obtained in zoological collections or provided by partner institutions (Lomonosov Moscow State University Marine Research Center and Shirshov Institute of Oceanology, Russian Academy of Sciences). A total of 213 grab samples were used to study biodiversity and variability of macrobenthos in two research areas in the Pechora Sea – the Pechora Bay and Vaigach Island. Assessment of video footage obtained using remotely operated vehicles revealed likely increasing in time presence of important benthic NIS snow crab *Chionoecetes opilio* (O. Fabricius, 1788) near Vaigach Island. Morphological analysis of stomach content was performed to characterise trophic niches of *C. opilio* and assess overlap with the diets of native benthic decapods, *Hyas araneus* (Linnaeus, 1758) and *Pagurus pubescens* Krøyer, 1838. Accumulation of microplastics in benthic invertebrates of the Pechora Sea was then assessed and compared with samples from the Kara Sea, Laptev Sea and East-Siberian Sea.

Macrobenthos of the continental shallows of the Pechora Bay were described for the first time in this thesis. A monodominant community of *Limecola balthica* (Linnaeus, 1758) comprised of eurythermal and euryhaline forms with reduced biomass, was shown to be at the margins of its distribution. In contrast, near Vaigach Island a high biomass, heterogeneous, macrobenthic community was found. During the six years of observations (2015–2020), the mean biomass, abundance, production and species composition fluctuated with no clear trends between years.

Twenty categories of prey items were identified in the diets of benthic decapods near Vaigach Island. Overlap in diets of the three species suggested that *C. opilio* likely competes for food resources with both *H. araneus* and *P. pubescens*. A conceptual diagram was generated to illustrate trophic interspecies relationships between benthic predators and macrobenthic communities in the Pechora Sea.

Microplastics were found to be a likely stressor on Arctic benthic ecosystems. Microplastic fibres were recorded in 29% of all samples of the Pechora Sea macrobenthos. Furthermore, an increase of average frequency of ingested microplastics in the field samples collected in 2017–2018 compared to the historical samples from 2008 was proved statistically significant. Similar occurrence of ingested microplastics were discovered in other studied regions of the Eurasian Arctic (average 27±2%). No significant differences in occurrence of ingested microplastics were identified between species, feeding guilds or sampling sites. A conceptual diagram was developed to illustrate microplastic ingestion by benthic fauna from different feeding guilds in the Pechora Sea.

Overall, the outcomes of this thesis provided valuable data, which are essential to review the current state of benthic biodiversity in the Pechora Sea, characterise the observed and expected impacts of key drivers of environmental change on benthic ecosystems, and provide recommendations including monitoring parameters and techniques, integration of which into the regional ecological monitoring programmes will lead to a more comprehensive understanding of the state and dynamics of the Pechora Sea benthic ecosystems. The Pechora Sea provides a case study illustrating the importance of incorporating data on benthic ecosystems into the marine spatial planning and specifically the design of marine protected areas, as well as the need for establishment of long-term ecological monitoring programmes with standardised approaches to data collection and interpretation to underpin the informed decision-making needed for sustainable development of the Arctic region.

Lay summary

The biodiversity of marine ecosystems of the Arctic Ocean is an "*irreplaceable cultural, scientific, ecological, economic and spiritual asset*" states the Arctic Biodiversity Assessment. In addition to its intrinsic value, Arctic biodiversity provides numerous ecosystem services and is crucial for indigenous people that rely on marine resources. At present the biodiversity of the Arctic is challenged by climate change and industrial development. Ecosystems that historically experienced only limited pressure from human activities are now facing new and emerging threats including rise in water and air temperatures, loss of sea ice habitats, introduction of nonindigenous species (NIS), anthropogenic pollution, increased methane emissions, seafloor habitat destruction, overfishing. Urgent actions are needed to protect Arctic biodiversity from individual and cumulative effects of these threats. Improvement of baseline knowledge to support informed decision-making, implementation of ecosystem-based management, identifying and protecting ecologically important areas are listed as priority actions to safeguard Arctic biodiversity.

Ecological monitoring is an integral mechanism in conservation and management of marine ecosystems, used to observe and characterise the status of ecosystems and determine how they change overtime. Seafloor communities of invertebrates (macrobenthos) are one of the essential components of biota used in monitoring as indicators of good environmental status. Macrobenthic communities are also focal ecosystem components as they provide feeding resources sustaining benthic predators of higher trophic levels. However, our knowledge of macrobenthic communities in the Arctic remains fragmentary and, in many regions, we lack even baseline data on biodiversity of benthic ecosystems, temporal variability of macrobenthic communities, individual and cumulative impacts of environmental stressors. This thesis aimed to help inform regional management and improve state of knowledge through assessing the status, variability and biodiversity conservation issues of Arctic benthic ecosystems of the ecologically significant area of the Barents Sea, the Pechora Sea.

I created a dataset of a total of 213 grab samples and 345 taxa of benthic invertebrates of the Pechora Sea through participating in a series of expeditions to the Pechora Sea with additional samples obtained in zoological collections or provided by partner institutions (Lomonosov Moscow State University Marine Research Center and Shirshov Institute of Oceanology, Russian Academy of Sciences). I used these data to assess biodiversity and variability of macrobenthos in two shallow-water (1–66 m) research areas in the Pechora Sea – the Pechora Bay and Vaigach Island. In addition, I used video footage obtained using remotely operated vehicles to assess frequency of

occurrence of mobile benthic megafauna and specifically the important benthic NIS snow crab *Chionoecetes opilio* near Vaigach Island. Trawl samples were used for morphological analysis of stomach content to characterise trophic niches of *C. opilio* and assess overlap with the diets of native benthic decapods in the area, *Hyas araneus* and *Pagurus pubescens*. In addition to diet composition, I assessed occurrence of microplastics in stomachs of *C. opilio* and other benthic invertebrates in the Pechora Sea and compared with microplastic occurrence in additional samples from the Kara Sea, Laptev Sea and East-Siberian Sea collected during the AMK-78 expedition in the Autumn of 2019.

The outcomes of the analyses of macrobenthos improve regional knowledge on macrobenthos of the Pechora Sea by providing comprehensive data on otherwise fragmentary described in literature Arctic shallow water benthic communities. More specifically, macrobenthos of the continental shallows of the Nenetsky State Nature Reserve in the Pechora Bay were described for the first time in this thesis. A low biomass and species richness estuarine community strongly dominated by *Limecola balthica* was discovered in the margins of its distribution. Extreme environmental conditions including fluctuations of temperature and salinity lead to paucity of benthos and presence of species that are more tolerable to changing conditions. In the second research area near Vaigach Island a rich in foraging biomass heterogeneous macrobenthic community was described. Two-thirds of the overall biomass were dominated by key prey items for benthic predators; bivalve species *Astarte borealis* (Schumacher, 1817), *Ciliatocardium ciliatum* (Fabricius, 1780) and *Astarte montagui* (Dillwyn, 1817). If their biomass extent is mainly driven by predator pressure, then biomass of these species can be used as an indicator parameter of foraging capacity of the area in future studies. During the six years of observations (2015–2020), the mean biomass, abundance, production and species composition fluctuated with no clear trends between the years. These results highlight the need to establish a long-term environmental monitoring programme to observe dynamics of macrobenthos along with dynamics of populations of benthic predators, and dynamics of the climate index in the wider Barents Sea area.

Analyses of the stomach contents of the megabenthic decapods revealed diverse non-specific diets of all three species formed by twenty categories of prey items and mostly comprised by macrobenthic species and plant debris. Diet composition of the three species overlapped, which suggests that the NIS *C. opilio* may compete for food resources with native benthic decapods. Outcomes of the video footage analyses revealed presence of the snow crab near Vaigach Island in 2016 and 2020. Interestingly, none of the male snow crabs sampled reached maturity according to the discriminant morphometric function which provides evidence to suggest that the Pechora Sea may have a role of nursery grounds. The snow crab is an important, commercially harvested species in the Barents Sea, however, the extent of monitoring programmes typically do not cover the Pechora Sea, therefore this thesis provides important new data on distribution, population structure and trophic role of the snow crab near Vaigach Island. A conceptual diagram was developed to illustrate complex trophic interspecies relationships between benthic predators and macrobenthic communities in the Pechora Sea.

Amongst the inclusions in the food lumps of benthic decapods, microplastic particles were registered and found to be an additional stressor on Arctic benthic ecosystems. On average, microplastic fibres were recorded in 27±2% of all 333 samples of macrobenthos from the Eurasian Arctic. I have also demonstrated that the average frequency of ingested microplastics in the field samples collected in 2017–2018 was significantly higher than in historical samples collected in 2008. No significant differences in occurrence of ingested microplastics were found between the species, feeding modes or sampling sites. I created a conceptual diagram to illustrate pathways of microplastic ingestion by macrobenthos in the Pechora Sea.

Overall, in this thesis I provided valuable new data improving the knowledge on the current state of benthic biodiversity in the Pechora Sea. I have also compiled recommendations including monitoring parameters and techniques, integration of which into the regional ecological monitoring programmes will help to form a more comprehensive understanding of the temporal variability of the Pechora Sea benthic ecosystems. Ultimately the Pechora Sea is an important case study illustrating the need for establishment of long-term ecological monitoring programmes with standardised approaches to data collection and interpretation to underpin the informed decision-making and sustainable use of marine resources in the Arctic region. The current nature conservation framework in Russia lacks effective mechanisms of integrating data on benthic ecosystems in marine spatial planning and these data are crucial and need to be taken into consideration specifically in the design of marine protected areas.

Author's Declaration

I certify that this thesis has been composed solely by myself and that it has not been submitted, in whole or in part, in any previous application for a degree or professional qualification in this or any other University. I confirm that the work submitted is my own, except where it is clearly stated otherwise by reference or acknowledgement. Where the presented work has formed a part of jointly authored publications (respective parts of chapters 2, 3, and 4), my contribution and contributions of other co-authors have been explicitly explained in the Research Integration section (1.3) of this thesis. The field data used in this study were collected by myself or provided by partner institutions (*Lomonosov Moscow State University Marine Research Center* and *Shirshov Institute of Oceanology, Russian Academy of Sciences*) as explained in Methods sections of each respective data chapters.

Anna Andreevna Gebruk

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I am equally grateful to the Lomonosov Moscow State University Marine Research Center who have provided invaluable support through the development of my career and enabled my participation in expeditions to the Pechora Sea in 2016–2018 where I collected field samples that formed core data of this thesis. Additional samples and data were collected with the help of Vladislav Kozlovsky and Vladimir Chava. I would like to highlight the enthusiastic support of the hydrobiology laboratory who have assisted me in identifying majority of the benthic samples and provided data for the other years of benthic surveys in the Pechora Sea to enable assessment of interannual variability of macrobenthos (specifically, Alexander Kokorin, Maria Fedyaeva and Maria Mardashova). I would also like to acknowledge support of the GIS department who have provided invaluable technical support in designing maps for this thesis (specifically, Yulia Ermilova, Polina Mikhaylukova and Marine Semenova). I am mostly grateful to Nikolay Shabalin and Olga Konovalova for supporting my decision to conduct this research whilst continuing my career in the LMSU MRC in parallel to my studies.

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Many new inspiring collaborations and opportunities have arisen through this journey and I am thankful to all my co-authors for their contributions to joint papers published as a part of this thesis (Gebruk et al., 2019; Gebruk et al., 2021a; Gebruk et al., 2021b; Gebruk et al., in press), as well as for an opportunity to contribute to some projects going beyond the scope of this thesis (Yakushev et al., 2021; Chava et al., 2021; Dgebuadze et al., 2021). I am also grateful to the field officers and vessel crews of all expeditions I have been so fortunate to take part in and collect samples for this thesis.

A final and very special thank you is reserved to my Mum (Irina Prokhorova) and Dad (Andrey Gebruk) whose unconditional love made me who I am, inspired me to become a marine scientist following my Dad's steps, enabled me to begin my PhD journey by providing emotional and financial support to move abroad and follow my dreams and supported me throughout the process from choosing the degree programme and drafting first application to handing in this thesis.

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Glossary

Abundance – total number of individuals of the species (or other taxonomic rank if specified) in the sample, typically standardised to an areal unit expressed in ind/m^2 (following statistical software manuals - Clarke and Warwick, 2001; Hammer and Harper, 2006; and regional literature on macrobenthos, e.g. - Zenkevich, 1927; Dahle et al., 1998; Denisenko et al., 2003; Kucheruk et al., 2003; Sukhotin et al., 2008; Denisenko, 2013).

Biomass– the weighted mass of all individuals of the species (or other taxonomic rank if specified) in the sample, typically standardised to an areal unit expressed in g/m^2 (in this study, wet biomass is used for field samples, following statistical software manuals - Clarke and Warwick, 2001; Hammer and Harper, 2006; and regional literature on macrobenthos, e.g. - Zenkevich, 1927; Dahle et al., 1998; Denisenko et al., 2003; Kucheruk et al., 2003; Sukhotin et al., 2008; Denisenko, 2013).

Euryhaline – species able to tolerate a wide range of salinity. In this thesis explained as species reported from different habitats with wide range of salinity gradients (marine, brackish, freshwater). Data derived from the World Register of Marine Species (WoRMS) and primary literature.

Eurythermal – species able to tolerate a wide range of temperature. In this thesis explained as species reported from different biogeographical regions (Arctic, boreal, temperate, subtropical). Data derived from the Ocean Biodiversity Information System (OBIS) and primary literature.

Feeding guild – a group of species of macrobenthos demonstrating similar feeding strategies, e.g., suspension feeders, deposit feeders, omnivores (feeding strategies reviewed in Cusson et al., 2005; Arapov et al., 2010; Macdonald et al., 2010)

Food lump – the stomach or gut content of the specimen containing food items and inclusions (food lump analysis method introduced by Burukovsky, 2009).

Invasive species – species that either show negative impact on recipient ecosystems or massive proliferation followed by an uncontrolled spread outside the natural distribution range (reviewed in Colautti and Richardson, 2009; Richardson et al., 2011; Riccardi et al., 2013).

Macrobenthos – free-living seafloor invertebrates, typically retained by a 1.0-mm-mesh sieve (Mare, 1942). The limit of detection in this study is 40 µm (the size of the metal strain for examination of the digested samples).

Macrobenthic community – a complex of species of macrobenthic invertebrates that occur together in the sample, defined by the dominant in biomass species (e.g., *Astarte borealis* – community), and distinguished from the other samples with statistical methods. This terminology is used following the regional literature on macrobenthos, e.g. - Zenkevich, 1927; Dahle et al., 1998; Denisenko et al., 2003; Kucheruk et al., 2003; Sukhotin et al., 2008; Denisenko, 2013 and statistical analysis guidance by Clarke and Warwick (2001).

Microplastics – plastic particles smaller than 5 mm in all measurable dimensions (GESAMP, 2019)

Non-indigenous species (NIS) – species observed outside of their recent natural distribution range (reviewed in Colautti and Richardson, 2009; Richardson et al., 2011; Riccardi et al., 2013).

Occurrence – in this thesis explained as proportion of the specimens of the species with the examined characteristic to all specimens of the species in the sample based on the presence/absence data matrix. E.g., occurrence of ingested microplastics - proportion of all specimens with ingested plastics to all study specimens.

Relative production – an approximated relationship between biomass and abundance data used to address input both from abundant but low in biomass species and larger organisms that dominate biomass but occur in samples less frequently. Expressed using the average exponent of annual relative production on body-size for macrobenthic invertebrates following Clarke and Warwick (2001). See Chapter 2.3.3 for formula.

List of Abbreviations

ABA	Arctic Biodiversity Assessment
AMAP	Arctic Monitoring and Assessment Programme
AMK	Akademik Mstislav Keldysh
AMSA	Arctic Marine Shipping Assessment
AMSP	The Arctic Council’s Arctic Marine Strategic Plan 2015-2025
ANOSIM	Analysis Of Similarities
AWI	Alfred Wegener Institute for Polar and Marine Research
BMW	International Convention for The Control and Management of Ships' Ballast Water and Sediments
BPA	Bisphenol A
CA	Nylon Cellulose Acetate
CAFF	Conservation Of Arctic Flora and Fauna
CBD	Convention On Biological Diversity
CBMP	Circumpolar Biodiversity Management Program
CH	Carapace Height (Depth)
ChH	Chela Height (Depth)
ChL	Chela Length
CIs	Clopper-Pearson Confidence Intervals
CL	Carapace Length
CW	Carapace Width
DDM	Degrees, Decimal Minutes
DF	Deposit Feeder
EBSA	Ecologically And Biologically Significant Marine Areas
EEZ	Exclusive Economic Zone
FECs	Focal Ecosystem Components
G	Grazer
GESAMP	Group Of Experts on The Scientific Aspects of Marine Environmental Protection
GOOS	Global Ocean Observing System
HDPE	High-Density Polyethylene
ILTER	International Long-Term Ecological Research Network
IMO	International Maritime Organisation
IMS	Industrial Methylated Solution
IO RAS	Shirshov Institute of Oceanology of The Russian Academy of Sciences
IPCC	The Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
LDPE	Low-Density Polyethylene
LME	Large Marine Ecosystem
LMSU MRC	Lomonosov Moscow State University Marine Research Center
LTER	Long-Term Ecological Research
MANOVA	Multiple Analysis of Variance
MMBI RAS	Murmansk Marine Biological Institute Russian Academy of Sciences
NIS	Non-Indigenous Species
nMDS	Non-Metric Multidimensional Scaling
OBIS	Ocean Biodiversity Information System
Om	Omnivores
OOI	Ocean Observatories Initiative
PA	Polyamide
PAHs	Polycyclic Aromatic Hydrocarbons
PAME	Protection Of the Arctic Marine Environment

PBDEs	Polybrominated Diphenyl Ethers
PCA	Principal Component Analysis
PCBs	Polychlorinated Biphenyls
PERMANOVA	Non-Parametric Multivariate Analysis of Variance
PET	Polyethylene Terephthalate
PINRO	Nikolai M. Knipovich Polar Research Institute of Marine Fisheries and Oceanography
PP	Polypropylene
PS	Polystyrene
PVC	Polyvinylchloride
PWP	Plastic Waste Partnership
QA/QC	Quality Assurance/ Quality Control
RD	Risk Differences
POP	Persistent Organic Pollutant
ROV	Remotely Operated Underwater Vehicle
RV	Research Vessel
SAON	Sustaining Arctic Observing Networks
SDF	Surface Deposit Feeders
SDG	United Nations’ Sustainable Development Goals
SEA_C	Small Sample Size Corrected Ellipses
SF	Suspension Feeder
SG	Strategic Goal
SIA	Stable Isotope Analysis
SIMPER	Similarity Percentage
SIOS	Svalbard Integrated Earth Observing System
SSDF	Subsurface Deposit Feeders
TAC	Total Allowable Catches
UNEP	United Nations Environmental Programme
UPGMA	Unweighted Pair Group Method with Arithmetic Mean
WHO	World Health Organisation
WoRMS	World Register of Marine Species
WWF	World Wide Fund For Nature
ZIN RAS	Zoological Institute of The Russian Academy of Sciences

Thesis Overview

Chapter focus

The thesis Overview briefly introduces regional context of the study, sets the overall thesis Objectives, explains the structure of the Data Chapters, and specifies the research approach and data integration, including sources of data, role of collaborating partners, and integration of papers published during this study, into this thesis.

Context of this study

Global climate change and industrial development pose major threats to Arctic biodiversity including but not limited to reduced sea ice extent and thickness, warming water and air temperatures, ocean acidification, habitat destruction, introduction of non-indigenous species and anthropogenic pollution including the introduction of plastics. Cumulative and long-term impacts of these stressors remain poorly understood. In addition, because of its remoteness, harsh conditions, scarce coastal population and historically low levels of industrial development, many areas of the Arctic Ocean still lack even baseline data on the state of ecosystems and improvement of knowledge on Arctic biodiversity is listed amongst the priority recommendations in the Actions for Arctic Biodiversity report by the Arctic Council (CAFF, 2015).

Arctic biodiversity is vital for sustaining livelihoods of indigenous people relying upon marine resources. In addition, connectivity is a key feature of the Arctic marine ecosystems, and biodiversity loss in the Arctic Ocean has unknown consequences for the resilience and health of the food webs in the adjacent regions of the World’s Ocean. Protection of Arctic marine ecosystems and biodiversity is now more prominently discussed in policy frameworks both internationally (e.g., the United Nations Convention on Biological Diversity, the United Nations Sustainable Development Goals of 2030; the Arctic Marine Strategic Plan 2015–2025 and Actions for Arctic Biodiversity 2013–2021 of the Arctic Council), and nationally (e.g., in the Russian Federation - Strategy and Executive Plan for the Conservation of Biodiversity in Russian Federation and the Strategy for the Development of the Arctic Zone of the Russian Federation and National Security up to 2035; in Norway – Arctic Strategy published by the Norwegian Ministry of Foreign Affairs in 2017). Furthermore, the ecosystem approach to management of human activities in Arctic marine and coastal environments was developed and endorsed by the Arctic Council (Kiruna Declaration, 2013; PAME, 2019) and in the core of this framework is informed decision-making based upon scientific evidence. Therefore, collecting baseline data on biodiversity and following monitoring of the state and trends of ecosystems are essential steps towards achieving biodiversity conservation targets in the Arctic.

Areas of heightened ecological significance in the Pechora Sea

The Pechora Sea in the south-eastern basin of the Barents Sea has unique marine ecosystems, different from the rest of the Barents Sea (Nikiforov et al., 2005; Sukhotin et al., 2019). Because of its remote location, partial isolation and influence of the continental run-off, the Pechora Sea is likely less directly impacted by the circulation of Atlantic water and global warming compared to the rest of the Barents Sea (Shishkin et al., 2020). In addition, unlike the majority of the Barents Sea, the Pechora Sea has historically experienced few anthropogenic pressures and no large-scale commercial fishery operations (Denisenko, 2013). However, some recent studies indicate pollution in the Pechora Sea, including elevated PCB in walrus tissues (Boltunov et al., 2019). Following the Arctic Council's 2009 Arctic Marine Shipping Assessment (AMSA, 2009) the entire Pechora Sea has been identified as an Area of Heightened Ecological Significance within the Large Marine Ecosystem (LME) of the Barents Sea due to its importance as spawning area for polar cod and herring, summer haul-outs for the Atlantic walruses, and migratory routes for marine birds (AMAP/CAFF/SDWG, 2013) (Figure 0-1).

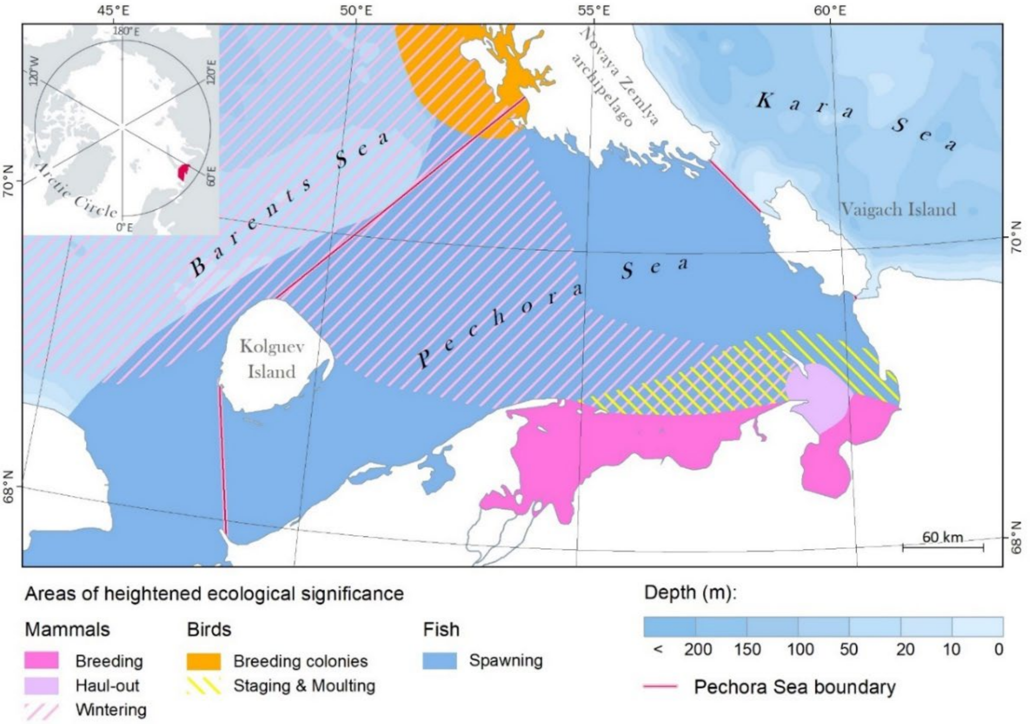


Fig. 0-1. Areas of heightened ecological significance in the Pechora Sea according to Arctic Marine Shipping Assessment (AMAP/CAFF/SDWG, 2013). Map courtesy of the LMSU MRC.

Importance of macrobenthic communities

Seafloor organisms (benthos) are prominently used in environmental monitoring as indicators of the state of marine ecosystems. These are mostly formed by infaunal long-living species (life spans on the order of years, and sometimes, decades). These are spatially stable and less affected by seasonal fluctuations in environmental conditions than pelagic species (Mokievsky and Tzetlin, 2020), thus benthic invertebrates are convenient for ecological monitoring. However benthic organisms rely on the supply of organic carbon from the sea surface, therefore, changes in advection processes impact the coupling of pelagic and benthic processes affecting species composition and biomass of benthic communities (Hunt et al., 2016). Typically, macrobenthic invertebrates retained by a 1.0-mm-mesh sieve are used in ecological monitoring (as opposed 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 ecosystem components due to their importance as foraging resources for benthic predators (CAFF, 2017). Arctic macrobenthos communities act as long-term integrators of changes in the environmental conditions (CAFF, 2013; CAFF, 2017).

In the Pechora Sea high levels of macrobenthic community biomass standing stock constitute important foraging grounds sustaining large feeding aggregations of marine sea ducks as well as the local population of walruses (Sukhotin et al., 2008; Semenova et al., 2019; Denisenko et al., 2019; Sukhotin et al., 2019). Existing marine protected areas in the Pechora Sea were designed to protect haul-out sites and moulting grounds and were established around the islands and coastlines, whereas benthic ecosystems that provide foraging resources for these species are not considered or systematically monitored. At the same time, Pechora Sea benthic ecosystems are facing increasing pressures from ongoing environmental change and industrial development and new emerging stressors such as marine pollution and invasion of non-indigenous species (the snow crab *Chionoecetes opilio*). However, our knowledge of the state of benthic communities, their interannual variability and impacts of these emerging threats on the state of benthic ecosystems remain fragmentary and this knowledge is essential for the sustainable development of the region.

Objectives and scope of this study

The **principle aim** of this thesis was to *assess the status, variability and biodiversity conservation issues of Arctic benthic ecosystems of the ecologically significant area of the Barents Sea, the Pechora Sea for improved management*, in the context of ongoing environmental change and future biodiversity conservation challenges. Furthermore, the ambition of this thesis was to develop suggestions for ecological monitoring based on most recent scientific evidence which will consider environmental stressors in the region and provide sufficient data to detect future changes in benthic ecosystems. Data collected through ecological monitoring are crucial for the development of marine spatial planning for the region that will enable sustainable practices of resource management. Recent reviews of different aspects of the Pechora Sea ecosystems highlighted a lack of integrity of data, particularly for the shallow-water benthic ecosystems, and the importance of biodiversity studies in providing baseline data for future conservation and sustainable management activities. Therefore, this thesis is tackling these issues by producing new data on the state and variability of the Pechora Sea benthic ecosystems and providing recommendations for best practices of ecological monitoring in the area.

Thesis Objectives

1) Characterise the current state of macrobenthos in the Pechora Sea (in the research areas underreported in literature).
2) Analyse interannual variability of biomass and community structure of macrobenthos in the Pechora Sea.
3) Assess occurrence of the non-indigenous snow crab *C. opilio* in the research area.
4) Characterise stomach contents and overlap in diets of the snow crab and native benthic decapods and suggest the trophic role of the snow crab in benthic trophic web of the Pechora Sea.
5) Identify levels of microplastic ingestion in macrobenthos of the Pechora Sea and assess spatial and temporal variation.
6) Provide recommendations for ecological monitoring of benthic ecosystems in the Pechora Sea with consideration of emerging stressors.

Thesis structure

The thesis consists of an Overall Introduction (Chapter 1), three Data Chapters (Chapter 2, Chapter 3, Chapter 4) and an overall Synthesis including conclusions and monitoring recommendations (Chapter 5).

Chapter 1 provided a rationale for this study and introduced key stressors that have an impact on Arctic marine ecosystems. It then established the regional setting of this thesis by reviewing main features distinguishing the Pechora Sea marine ecosystems from the rest of the Barents Sea. The Introduction also provided a historical review of benthic research in the Barents Sea identifying key knowledge gaps and less represented areas. Lastly, Chapter 1 reviewed the current conservation status of Pechora Sea ecosystems highlighting features and functions of heightened ecological significance following the Arctic Council reports.

Data Chapter 2 characterised the current state and interannual variability of macrobenthic communities of the Pechora Sea. The chapter began with an introduction to temporal variability of macrobenthos, focusing on ecological theories explaining temporal change in macrobenthos and why macrobenthos are used in environmental monitoring. Description of the current state of macrobenthos provided extensive and up-to-date data on biodiversity, biomass and abundance of macrobenthic communities in the shallow water areas of the Pechora Sea, including the first description of shallow water macrobenthos of the Pechora Bay and extensive study of structure of benthic communities near Vaigach island, in the key foraging grounds of Atlantic walruses. Interannual variability of macrobenthos was assessed based on the data collected in field campaigns near Vaigach Island in 2015–2020. Potential drivers of change in regional macrobenthos are then discussed.

Data Chapter 3 addressed the role of the non-indigenous species (NIS) of benthic decapod, the snow crab *Chionoecetes opilio*, in the benthic trophic web of the Pechora Sea. The introduction of this chapter began with a broader discussion of effects of biological invasions on marine trophic webs, then it provided context to NIS in the Arctic and the invasion of the snow crab in the Barents Sea. Trophic niche of the snow crab in the Pechora Sea was then assessed through stomach content analyses and compared to diets of native benthic decapods in the area to check for potential overlap and trophic competition. Specimens for the diet analyses were obtained during the RV *Kartesh* research expedition to the Pechora Sea in 2017. In addition, analyses of footage from remotely operated underwater vehicle (ROV) were conducted to review abundance of the snow crab and relative fraction of sow crabs to all decapods in the research area in 2016 and 2020. Lastly, a conceptual diagram of trophic interspecies interaction was suggested and discussed.

Data Chapter 4 focused on emerging pollutants and investigated accumulation of microplastics in benthic ecosystem of the Pechora Sea. In this Chapter, three groups of samples of macrobenthos were studied for microplastic ingestion: (1) field samples collected from the Pechora Sea in 2017–2018 to assess the baseline level of microplastic ingestion in the Pechora Sea; (2) historic samples from zoological collections of Institute of Oceanology collected from the Pechora Sea in 2008 were studied to assess temporal change in accumulation of microplastics; (3) field samples collected from the Kara Sea, Laptev Sea and East-Siberian Sea in 2019 were assessed to compare microplastic pollution the Pechora Sea with other regions of the Arctic. A conceptual diagram of accumulation of microplastics in benthic ecosystem of the Pechora Sea was presented and discussed. Chapter 4 presented the first investigation on marine microplastics in macrobenthos of the Pechora Sea. Further research questions were defined for future studies of benthic microplastics in the Eurasian Arctic and in the Pechora Sea.

Chapter 5, an overall synthesis with conclusions and recommendations for monitoring was focused on the key environmental and anthropogenic factors that are posing threats to biodiversity of the benthic ecosystems of the Pechora Sea and provided recommendations on how to monitor impacts of these stressors on benthic communities to detect changes. Emerging threats in the Pechora Sea include introduction of non-indigenous species and marine plastic pollution alongside the ongoing sea ice retreat and intensification of human activities. In that respect, the Pechora Sea provided an important case study illustrating the need to incorporate data on benthic ecosystems into the informed decision-making in the Arctic and specifically in the design of marine protected areas.

Research approach and data integration

Data sources

Core data on macrobenthic communities of the Pechora Sea used in this thesis were collected during the RV *Kartesh* expeditions to the Pechora Sea in 2015-2020 organised by the Lomonosov Moscow State University Marine Research Center (LMSU MRC). Samples were collected during the expeditions in 2016–2018 by the author, additional samples from 2015, 2019 and 2020 expeditions were provided for this study by the LMSU MRC (namely, Nikolay Shabalin, Vladislav Kozlovsky, Vladimir Chava and Alexander Kokorin). Macrobenthic invertebrates collected during the RV *Kartesh* expeditions were collected with the bottom grabs (*Okean-0.1*; *Okean-50*) and scientific trawl (*Sigsbee*), all washed over a 0.5 mm mesh with seawater and preserved in 4% formaldehyde solution. In addition, in 2016 and 2020 ROV video recordings were taken during the expeditions by ROV operators Vadim Aleskerov and Vladimir Chava and used for assessment of the snow crab abundance presented in Chapter 3 of this thesis.

Macrobenthic samples from the Pechora Bay analysed in Chapter 2 were collected during the coastal expedition to the Nenetsky State Nature in August 2016. Samples were collected from a motorboat with a hand shovel with capture area of 0.05 m^2 by author. Taxonomical identification of macrobenthic invertebrates from the samples collected in 2016 (from the Pechora Bay and near Vaigach Island) was carried out by author, the rest of the macrobenthic samples were identified by the taxonomy specialists of hydrobiology laboratory of LMSU MRC.

Decapod specimens were collected from the trawl samples during the RV *Kartesh* expeditions to the Pechora Sea in 2017–2018. Samples for diet analyses were collected, measured and further processed by author following procedure described in Chapter 3 (Section 3.3.3 – Data analysis).

Additional samples for microplastic ingestion analysis (Chapter 4) were collected by author during the *AMK-78* expedition to the Russian Arctic in September-October 2019 from the Kara, Laptev and East-Siberian Seas. Historical samples used for analyses of temporal variation of microplastic ingestion were taken from zoological collections of the Shirshov Institute of Oceanology of the Russian Academy of Sciences (IO RAS). Samples for microplastic analysis were identified and processed by author following procedure described in the Methods section in Chapter 4.

All data handling and analyses were conducted by the author of this thesis using the free statistical software PAST version 3.22 (Hammer and Harper, 2006): specific statistical tools are described in the Methods sections of respective data Chapters (Sections 2.3; 3.3; 4.3).

Appendix 0-1 consolidates attributes of all sampling sites used in this thesis including the year and date of sampling, sampling gear used and number of repeats, geographical coordinates and water depth at the site. Figure 0-2 illustrates the position of all sampling sites with different colours of dots representing different sampling gear as explained in the legend.

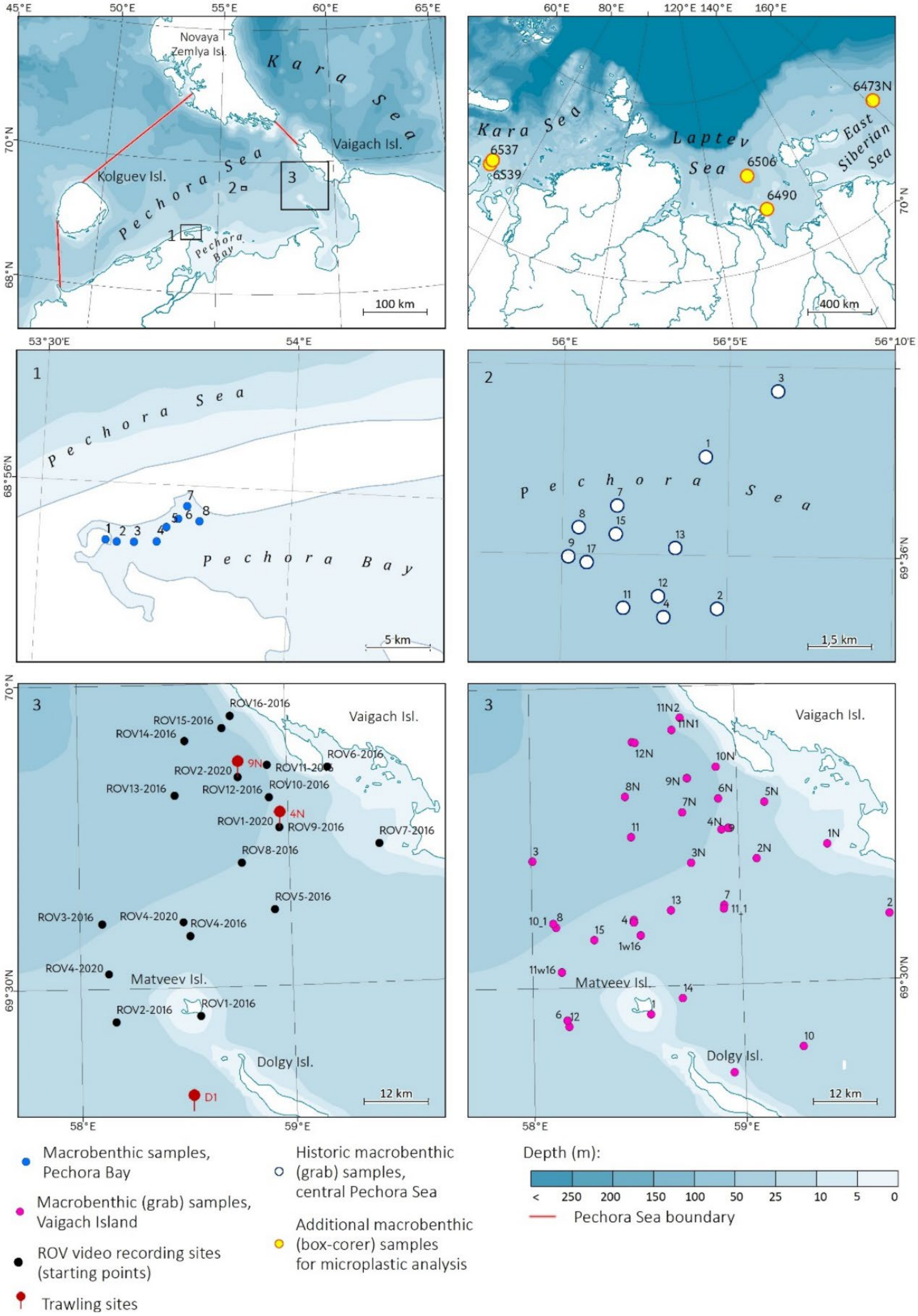


Fig. 0-2 Position of all field sampling sites. Black rectangles show the research areas (1) Vaigach Island; (2) The central Pechora Sea; (3) The Pechora Bay. The colourful dots (blue, pink, white) mark sites of sampling macrobenthos. Black labelled dots show the starting points of ROV video recordings and red dots mark stating points of the trawling samples. Yellow dots show sites where box-corer samples were collected during the *AMK*-78 expedition. Numbers refer to the code of sampling site in field journals.

Co-authored publications

I intend to publish key outcomes of this thesis in peer-reviewed scientific journals. As of summer 2021, three papers have been already published (Gebruk et al., 2019; Gebruk et al., 2021a; Gebruk et al., 2021b), one paper is accepted for publication in 2021 (Gebruk et al., in press), and one paper is in preparation. My research contribution and contribution of other co-authors to the jointly authored published papers described below for each paper.

- *Gebruk et al., 2019*

Full citation: Gebruk AA, Borisova PB, Glebova MA, Basin AB, Simakov MI, Shabalin NV, Mokievsky VO (2019) Macrozoobenthos of the shallow waters of Pechora Bay (SE Barents Sea). *Nature Conservation Research* 4(4), 1–11

DOI: https://doi.org/10.24189/ncr.2019.058

Gebruk et al. (2019) is a research article providing first description of the shallow water macrobenthos of the Pechora Bay within the near-shore zone of the Nenetsky State Nature Reserve. The paper characterises species diversity, abundance and biomass of macrobenthos from the eight sites sampled in the Pechora Bay in August 2016. As a leading author of this paper, I have carried out sampling, samples identification, data analyses and write up of the paper. Contribution of other co-authors included verification of identification of macrobenthic invertebrates (Alexander Basin, Miloslav Simakov); assistance in the design of the study (Nikolay Shabalin, Vadim Mokievsky); creating of GIS maps (Milana Glebova); review and editing of the manuscript text (all). Main text of this manuscript (Gebruk et al., 2019) was developed as a part of Chapter 2 of this thesis (included in sections 2.4.1 and 2.5.1).

- *Gebruk et al., 2021a*

Full citation: Gebruk A, Mikhaylyukova P, Mardashova M, Semenova V, Henry L-A, Shabalin N, Narayanaswamy B & Mokievsky V (2021a) Integrated study of benthic foraging resources for Atlantic walrus (*Odobenus rosmarus rosmarus*) in the Pechora Sea, south-eastern Barents Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems* 31(1): 112–125

DOI: https://doi.org/10.1002/aqc.3418

The aim of this paper (Gebruk et al., 2021a) was to examine the distribution and diversity of benthic foraging resources used by the Atlantic walrus in the Pechora Sea in its key foraging grounds near Vaigach Island. The paper integrates multiple sources of environmental and biological data collected by satellite telemetry, remotely operated vehicle (ROV) and benthic grab sampling. Satellite telemetry data were provided and analysed by Varvara Semenova and were not included in this thesis. My contribution as a leading author in this paper included collecting and processing macrobenthic samples (identification together with Maria Mardashova); analysis of macrobenthic data; analysis of ROV video recordings; write up of the full manuscript. Contribution of other co-authors in addition to those named above included assistance in the design of the study (Lea-Anne Henry; Nikolay Shabalin, Vadim Mokievsky); creating of GIS maps (Polina Mikhaylyukova); review and editing of the manuscript text (all). In this thesis outcomes of Gebruk et al., 2021a are included in Chapter 2 (Section 2.4.2 – Macrobenthos near Vaigach Island in 2016) and Chapter 3 (Section 3.4.1 – Occurrence of the snow crab in the Pechora Sea). It is important to add, that in Chapter 3 data from this paper are combined with the new ROV data obtained in 2020 and analysed together. Outcomes of the analyses of temporal variability of macrobenthos presented in Chapter 2 (Results Section 2.4.3 – Interannual variability of macrobenthos in the Pechora Sea) are currently being developed into a separate research paper that I intend to submit later in 2021.

- *Gebruk et al., 2021b*

Full citation: Gebruk A, Zalota AK, Dgebuadze P, Ermilova Y, Spiridonov VA, Shabalin N, Henry L-A, Henley S, Mokievsky V (2021b) Trophic niches of benthic crustaceans in the Pechora Sea suggest that the invasive snow crab *Chionoecetes opilio* could be an important competitor. *Polar Biology* 44(1): 57–71

DOI: https://doi.org/10.1007/s00300-020-02775-3

In this study, an integrated approach was used combining stomach content analysis and stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) to examine the trophic niches of three decapod species in the Pechora Sea – the invasive snow crab *Chionoecetes opilio* and two species of native decapods, the spider crab *Hyas araneus* and the hermit crab *Pagurus pubescens*. Decapod samples studied in this paper were collected during the RV *Kartesh* expeditions to the Pechora Sea in 2017–2018. As a leading author of this paper, I have collected decapod specimens, measured, dissected and processed the samples (e.g., conducted stomach content (diet) morphological analysis), carried out data interpretation, and full manuscript text write up. Stable isotope analysis was conducted by Anna Zalota and not included as a part of this thesis (except in the discussion of Chapter 3 with the appropriate referencing). Maps were created by Yulia Ermilova. Other co-authors contributed to the study design, review and editing of the manuscript. In this thesis the stomach content analyses of the Pechora Sea benthic decapods are included in Chapter 3 (Results Section 3.4.2 – Stomach content analyses).

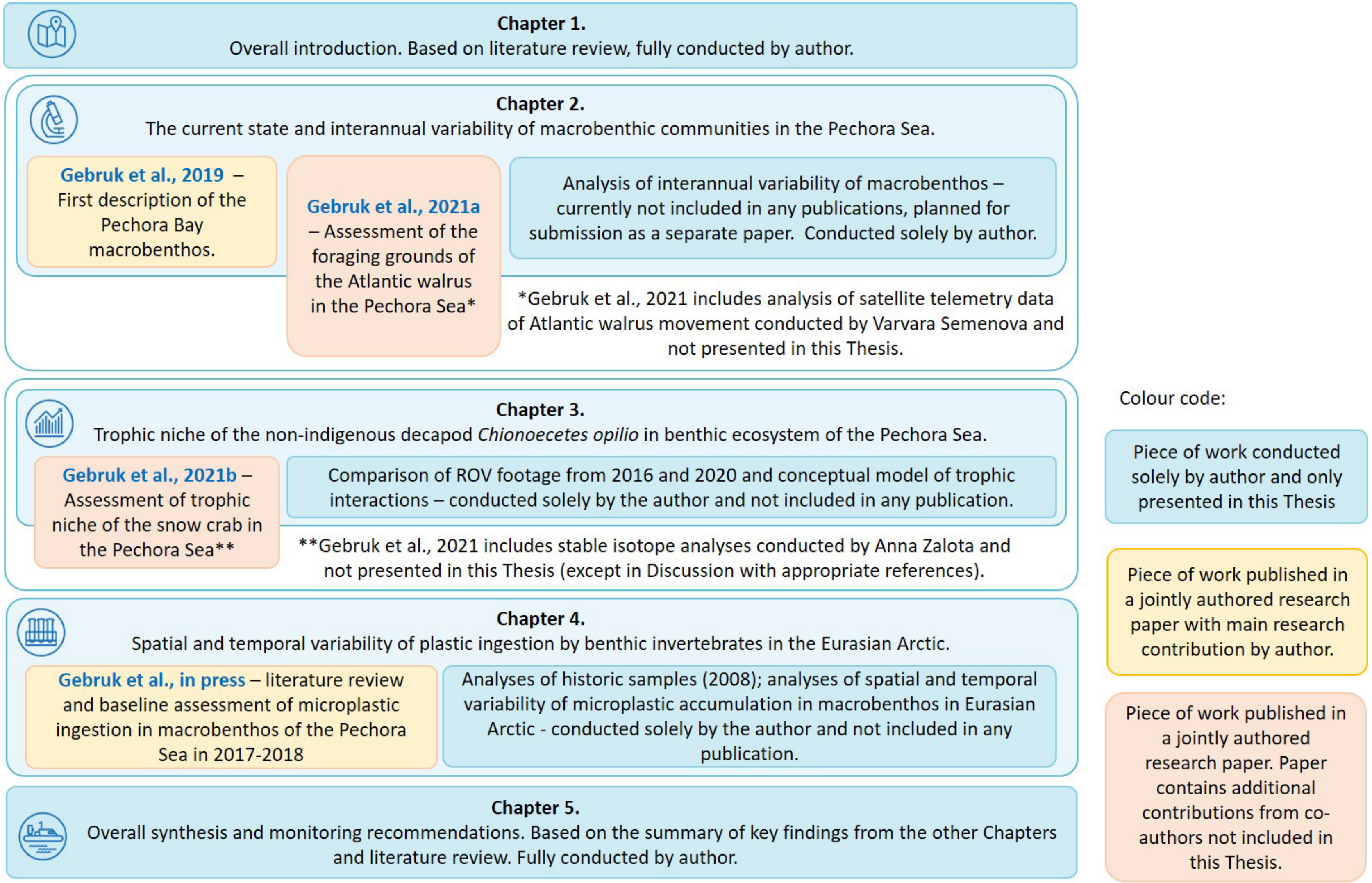
- *Gebruk et al., in press*

Full citation: Gebruk A, Ermilova Y, Henry L-A, Henley S, Spiridonov V, Shabalin N, Osadchiev A, Yakushev E, Semiletov I, Mokievsky V (In Press) Microplastics in the Arctic benthic fauna: a case study of the snow crab in the Pechora Sea, Russia. In: Informed Decisionmaking for Sustainability. Volume 2. Building Common Interests in the Arctic Ocean with Global Inclusion. (Editors: Paul Arthur Berkman, Oran R. Young, Alexander N. Vylegzhanin, David A. Balton and Ole Øvretveit). Springer.

DOI: not yet assigned

This paper includes an extensive literature review of marine microplastics and their interactions with marine biota (included in Chapter 1 of this thesis) and initial results on microplastics ingestion by nine species of benthic fauna from the Pechora Sea collected during the RV *Kartesh* expeditions in summer 2017 and summer 2018. As a first author of this paper, I have collected and processed the samples, carried out data interpretation, literature review, and write up of the manuscript. Other co-authors contributed to the study design, review and editing of the manuscript (all) and GIS mapping (Yulia Ermilova). Baseline assessment of microplastic ingestion by macrobenthos in the Pechora Sea is presented in Chapter 4 of this thesis (Results Section 4.4.2 – Occurrence of ingested microplastics in macrobenthos). However, the scope of Chapter 4 of this thesis extends beyond the scope of the paper as spatial and temporal variability of microplastic ingestion were also investigated and additional samples obtained from zoological collections of IO RAS and during the *AMK*-78 expedition to the Kara, Laptev and East-Siberian Seas in 2019.

Figure 0-3 demonstrates how the co-authored papers discussed above are integrated in the structure of this thesis, the diagram also indicates additional data and analysis presented in the Chapters building upon the published papers.



Chapter 1.
Overall introduction. Based on literature review, fully conducted by author.

Chapter 2.
The current state and interannual variability of macrobenthic communities in the Pechora Sea.

Gebruk et al., 2019 – First description of the Pechora Bay macrobenthos.

Gebruk et al., 2021a – Assessment of the foraging grounds of the Atlantic walrus in the Pechora Sea*

Analysis of interannual variability of macrobenthos – currently not included in any publications, planned for submission as a separate paper. Conducted solely by author.

*Gebruk et al., 2021 includes analysis of satellite telemetry data of Atlantic walrus movement conducted by Varvara Semenova and not presented in this Thesis.

Chapter 3.
Trophic niche of the non-indigenous decapod *Chionoecetes opilio* in benthic ecosystem of the Pechora Sea.

Gebruk et al., 2021b – Assessment of trophic niche of the snow crab in the Pechora Sea**

Comparison of ROV footage from 2016 and 2020 and conceptual model of trophic interactions – conducted solely by the author and not included in any publication.

**Gebruk et al., 2021 includes stable isotope analyses conducted by Anna Zalota and not presented in this Thesis (except in Discussion with appropriate references).

Chapter 4.
Spatial and temporal variability of plastic ingestion by benthic invertebrates in the Eurasian Arctic.

Gebruk et al., in press – literature review and baseline assessment of microplastic ingestion in macrobenthos of the Pechora Sea in 2017-2018

Analyses of historic samples (2008); analyses of spatial and temporal variability of microplastic accumulation in macrobenthos in Eurasian Arctic - conducted solely by the author and not included in any publication.

Chapter 5.
Overall synthesis and monitoring recommendations. Based on the summary of key findings from the other Chapters and literature review. Fully conducted by author.

Colour code:

Piece of work conducted solely by author and only presented in this Thesis

Piece of work published in a jointly authored research paper with main research contribution by author.

Piece of work published in a jointly authored research paper. Paper contains additional contributions from co-authors not included in this Thesis.

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Gebruk A, Zalota AK, Dgebuadze P, Ermilova Y, Spiridonov VA, Shabalin N, Henry L-A, Henley S, Mokievsky V (2021) Trophic niches of benthic crustaceans in the Pechora Sea suggest that the invasive snow crab *Chionoecetes opilio* could be an important competitor. *Polar Biology* 44(1): 57–71

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Chapter 1. General Introduction

Chapter focus

The Introduction chapter provides context to the importance of protection of biodiversity in the Arctic by introducing key stressors, recent and anticipated Arctic climate and environmental change, and anthropogenic pressures. It then introduces the regional setting, explaining conservation status, key features and state of knowledge on the Pechora Sea marine ecosystems with specific focus on a historic review of the available literature data on macrobenthos.

> *“The unprecedented changes being experienced in the Arctic emphasize the importance and urgency of getting information to decision-makers in a timely manner. <…> As data on this scale are only available for a few well-known species and ecosystems, it is not possible to provide a comprehensive accounting of status and trends of all Arctic biodiversity” (CAFF, 2013).*

1.1. Introduction to Arctic biodiversity, key stressors and conservation priorities

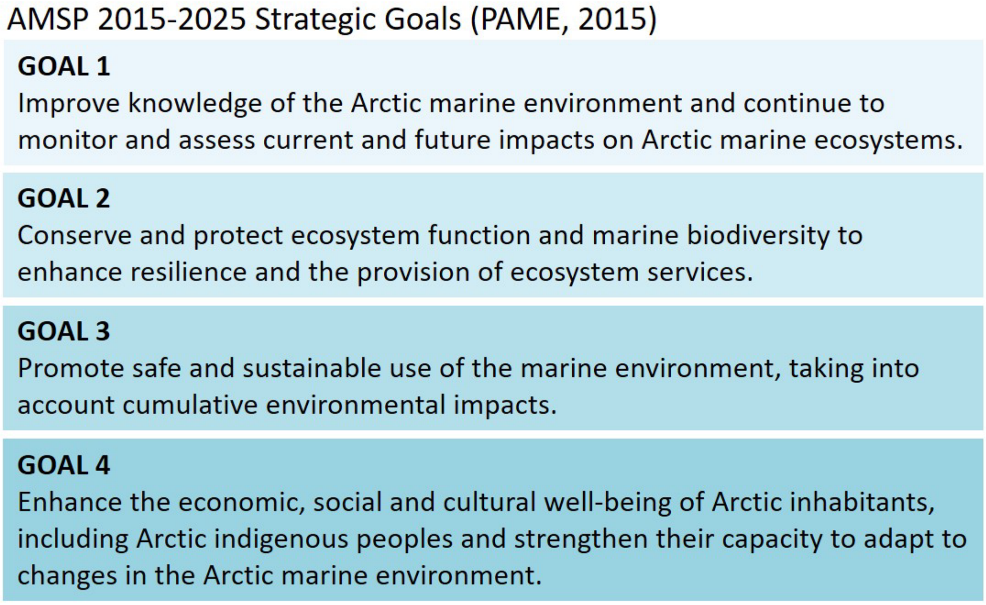
1.1.1. Importance of Arctic marine ecosystems and biodiversity

“Arctic biodiversity is an irreplaceable cultural, scientific, ecological, economic and spiritual asset” states the Arctic Biodiversity Assessment: Report for Policy Makers (CAFF, 2013). The Arctic is home to numerous species with unique adaptations to specific habitats (e.g., sea ice) and conditions including limitations in light availability, extreme cold and seasonality (e.g., anti-freeze substances in the body fluids in cold-blooded animals as an adaptation to subzero temperatures). Despite the physical environmental constraints, the Arctic shelf sustains some of the most productive marine ecosystems on Earth in terms of primary production and provides invaluable ecosystem services to people relying upon marine resources on local, regional and global scales (CAFF, 2013). Changes in environmental conditions can have an impact on abundance, distribution ranges, food availability or habitat suitability of certain species affecting the ecosystem’s stability. The speed and size of the environmental change, including the oceanic warming observed in the polar regions over the last decades and in the last century, is unprecedented for the climate records (Barnes and Tarling, 2017). The Atlantic inflow is the main vector of oceanic heat transport into the Arctic, and it is predicted to continue to increase under future climate warming (e.g., Hunt et al., 2016). In the atmosphere, rising temperatures globally increase the latent heat transport, leading to warming of the lower troposphere in the polar regions (Hunt et al., 2016). Due to the polar amplification effect, climate change accelerates in the high latitudes at a higher rate than anywhere on Earth (IPCC, 2014; IPCC, 2021) making it by far the most serious threat to Arctic biodiversity. More specifically, the temperature of the Arctic warmed at twice the rate of the global average (2℃ increase since 1850 compared with 1℃ globally) and is projected to further increase by at least another 1℃ on average and by 2℃ in the Atlantic sector even under the most optimistic climate scenarios (Hunt et al., 2016; CAFF, 2017; Siegert et al., 2020). With medium confidence, a nearly ice-free Arctic Ocean in summer is projected by the mid-21st century (IPCC, 2014; Hunt et al., 2016; IPCC, 2021). This, together with new and growing anthropogenic pressures being brought to the region with the industrial development of coastal infrastructures and marine industries, lead to degradation of Arctic biodiversity and acute need for decisive action. It is also important to highlight that connectivity of the Arctic with the other areas of the World's Ocean and specifically the North Atlantic and the North Pacific through circulation of the water masses, and array of chemical, physical and biological interactions, makes preservation of healthy, productive and resilient marine ecosystems in the Arctic a matter of global significance.

Many reports, assessments and action plans produced by the working groups of the Arctic Council mandate the urgent need to protect the integrity of Arctic biodiversity, including the following reports listed in chronological order:

- Arctic Marine Shipping Assessment (PAME, 2009);
- Arctic Biodiversity Assessment (CAFF, 2013);
- Identification of Arctic marine areas of heightened ecological and cultural significance: Arctic Marine Shipping Assessment (AMAP/CAFF/SDWG, 2013);
- The Arctic Council's Arctic Marine Strategic Plan 2015–2025 (AMSP) (PAME, 2015a);
- Framework for a Pan-Arctic Network of MPAs (PAME, 2015b)
- State of the Arctic Marine Biodiversity Report (CAFF, 2017);
- Guidelines for Implementing an Ecosystem Approach to Management of Arctic Marine Ecosystems (PAME, 2019a);
- Desktop study on marine litter including microplastics in the Arctic (PAME, 2019b).

One of the fundamental conclusions of these reports is that the current state of knowledge on marine ecosystems and biodiversity in the Arctic remains fragmentary and often insufficient for effective science-based decision-making. Therefore, improving and expanding the knowledge-base and monitoring the status and trends of Arctic biodiversity is listed as the first goal of the Arctic Marine Strategic Plan 2015–2025 (AMSP) (PAME, 2015a). Strategic goal (SG) 2 states the need to protect marine biodiversity and ecosystem functions, and the remaining two strategic goals relate to sustainable use of marine resources and well-being of Arctic inhabitants (PAME, 2015a; Figure 1.1-1).



AMSP 2015-2025 Strategic Goals (PAME, 2015)

GOAL 1
Improve knowledge of the Arctic marine environment and continue to monitor and assess current and future impacts on Arctic marine ecosystems.

GOAL 2
Conserve and protect ecosystem function and marine biodiversity to enhance resilience and the provision of ecosystem services.

GOAL 3
Promote safe and sustainable use of the marine environment, taking into account cumulative environmental impacts.

GOAL 4
Enhance the economic, social and cultural well-being of Arctic inhabitants, including Arctic indigenous peoples and strengthen their capacity to adapt to changes in the Arctic marine environment.

Fig. 1.1 - 1. Strategic Goals of the 2015–2025 Arctic Marine Strategic Plan (based on PAME, 2015a).

More specific actions have been identified later by the Conservation of Arctic Flora and Fauna (CAFF) working group to address conservation of Arctic biodiversity in the “actions for biodiversity” report (CAFF, 2015), including the following – (1) improving knowledge and public awareness; (2) tackling climate change; (3) implementation of ecosystem-based management; (4) identifying and safeguarding important areas for biodiversity; and (5) addressing individual stressors on biodiversity and their cumulative impacts. This thesis is focused on assessing the understudied Arctic shallow-water benthic ecosystems of the Pechora Sea and providing recommendations for monitoring of benthic biodiversity and state of ecosystems, and it therefore contributes to SG1 and SG2 of the AMSP by both improving regional knowledge and promoting biodiversity conservation.

1.1.2. Key stressors of Arctic biodiversity

Anthropogenic pressures on marine ecosystems continue to grow, and alongside the climate change and changing environmental conditions they lead to decreasing biodiversity and loss of habitats globally (Korpinen and Andersen, 2016). However still little is known about spatial patterns of these stressors and their cumulative impacts (Halpern et al., 2015). This applies especially to the Arctic region where limited accessibility and extreme weather conditions historically led to scarce coastal population and relatively low human influence, as well as fragmentary state of knowledge on ecosystems and biodiversity.

Ongoing climate change and intensification of offshore industries subsequently increase pressures on unique Arctic biodiversity. Key stressors of Arctic biodiversity have been divided by CAFF into three principal categories: (1) physical drivers of change; (2) human drivers of change; and (3) cumulative impacts of multiple stressors as listed in Table 1.1-1 below.

Table. 1.1 - 1. Key physical and human drivers of change in the Arctic and their effects on marine ecosystems according to State of the Arctic Marine Biodiversity Report (CAFF, 2017).

	Stressor	Effects on marine ecosystems and biodiversity
Key physical drivers of change in the Arctic		
1.1	Sea surface temperature	Effects for marine biota (changing life cycles, predator-prey relations, distribution, population cycles, breeding and feeding activity, etc)
1.2	Ocean currents and frontal boundaries	Thermal barriers for species distribution, changes in food and nutrient availability
1.3	Sea surface salinity	Alterations in physical and chemical environment, affecting ocean currents and potentially affecting food webs
1.4	Ocean acidification	Severe impact on biota depending on chemical carbonate balance (e.g., pteropods)
1.5	Nutrients	Changes in food webs, ecosystem shifts
1.6	Sea ice (ice cover, ice concentration, ice dynamics, marginal ice zones, polynyas)	Seasonal light availability, water temperature and flow of energy, phytoplankton blooms and dynamics of food webs, productivity
Key human drivers of change in the Arctic		
2.1	Harvest and fisheries	Direct impacts (mortality, population demographic shifts); indirect impacts (bycatch, habitat loss, disturbance, alterations of prey availability etc
2.2	Persistent, bio-accumulative and toxic contaminants	Ecotoxicological effects on marine biota from persistent organic pollutants (POP), toxic metals, plastics and microplastics
2.3	Industrial development	Habitat loss, alteration, disturbance, oil spills, pollution, noise, etc
2.4	Shipping	Oil spills, chemical discharges, waste, noise pollution, collision with marine mammals, introduction of alien species, etc
2.5	Invasive alien species	Effects on food webs, biodiversity loss, ecosystem shifts
Cumulative effects		
3	Cumulative effects of multiple stressors (including interactions between combinations of stressors)	Largely unknown but likely increased negative impacts

Although all listed stressors have an impact on biodiversity in the entire Arctic Ocean, their relative importance and scale of impact depend on regional oceanographic and ecological setting.

The focus of this study is the benthic realm of the Pechora Sea, which corresponds to the Barents Sea large marine ecosystem (LME) (AMAP/CAFF/SDWG, 2013) or the Barents Sea ecoregion (Larsen et al., 2004). A specific list of the key environmental stressors in the Barents Sea ecoregion was identified in biodiversity assessment by the WWF (Larsen et al., 2004). The list included the combination of the following physical and anthropogenic parameters (Larsen et al., 2004):

- Climate change. Specifically, the consequences of the temperature rise and sea ice decline on species distribution ranges, abundance and composition potentially leading to ecosystem shifts.
- Overfishing. Related issues include bycatch, habitat destruction through bottom trawling, food availability for higher trophic levels.
    - Aquacultures. WWF raises specific concerns related to the growth of aquaculture industry in the region including (1) large numbers of wild fish needed to sustain farmed fish contributing to overfishing issues in the region; (2) poor management of some fish farms and related risks of nutrient, chemical and pathogen release into the environment; (3) insufficient protection of vulnerable marine and coastal ecosystems in the areas of development of fish farms.
- Offshore oil and gas developmen*t.* Risks of oil spills, pipeline leaks, discharge of drilling chemicals, noise pollution, infrastructure development and related habitat destruction.
- Shipping. Risk of collisions with marine mammals, acoustic disturbance, increased pollution, transportation of non-indigenous species through ballast waters and biofouling - these risks are particularly relevant in the context of rapid development of the northern sea route.
- Long-range pollution as result of the global thermohaline circulation, continental run-off and partial geographic isolation of the Barents Sea from the rest of the Eurasian Arctic (Novaya Zemlya archipelago and Vaigach Island on the border with Kara Sea). The Barents Sea often referred to as a “sink” for long-range pollution in the Arctic including POP, heavy metals and plastics.
    - Radioactivity - nuclear waste is highlighted by WWF as a major threat in the Barents region due to the high density of nuclear plants in the Kola peninsula.
- Introduction of alien species: the biodiversity assessment highlights ecosystem damage from the invasive king crab introduced in the Barents Sea in the 1960s and reviewed in more detail in Chapter 3.

Further narrowing down the list of key threats to biodiversity specifically for the Pechora Sea marine ecosystems is complicated as little research has been focusing solely on the ecosystem stressors of the Pechora Sea. Despite the substantial body of literature dedicated to different aspects of the environmental conditions, marine ecosystems and geological history of the Pechora Sea (reviewed in Bauch et al., 2005; Denisenko, 2013; Sukhotin et al., 2019), less attention has been drawn to ecosystem dynamics, biodiversity threats and management implications. The recent issue of the *Polar Biology* journal dedicated to the Pechora Sea ecosystems highlighted anthropogenic pollution, offshore oil and gas production, increasing maritime transport, introduction of non-indigenous species and climate change (leading to air temperature rise, loss of sea ice habitats, increased frequency of storm events, increased continental run-off) as major modern threats to the integrity of the Pechora Sea ecosystems, which historically experienced low anthropogenic impacts and negligible baseline contamination (Sukhotin et al., 2019).

1.2. Introduction to the study area and regional setting

1.2.1. Key features of the Pechora Sea marine ecosystems

The Pechora Sea is a vernacular name of a semi-enclosed area water territory in the south-east basin of the Barents Sea surrounded by Kolguev Island from the west, Novaya Zemlya archipelago from the north, and Vaigach Island from the east, covering a total area of approximately 90,000 km^2 (corresponding to nearly 10% of the total Barents Sea area) (Figure 1.2-1). On the east the Pechora Sea is adjacent to the Kara Sea, the two seas are connected through the two straits, the Kara Gate and the Yugorsky Shar. The Pechora Sea is named after the Pechora River which forms a large bay and acts as an important transport vein for maritime traffic entering the Northern Sea Route from the continent.

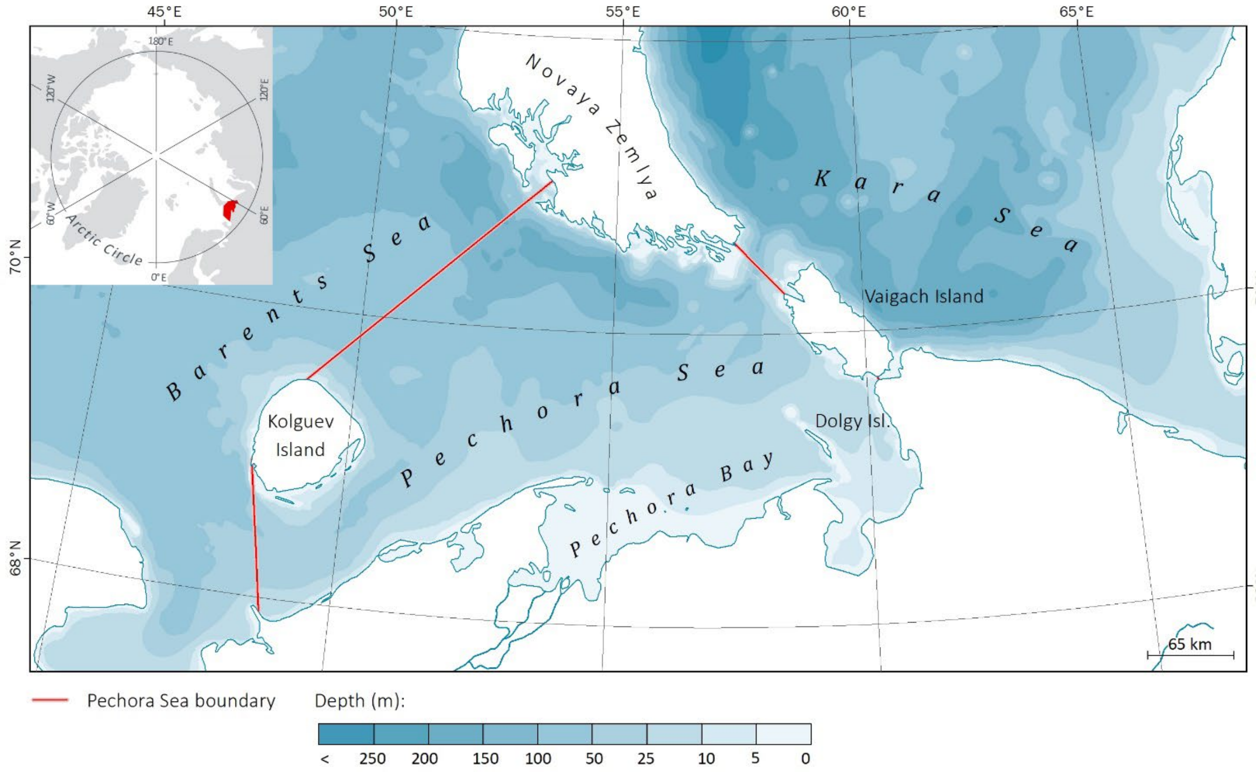


Fig. 1.2 - 1. Geographical location and boundaries of the Pechora Sea. Map courtesy of the LMSU MRC.

Marine ecosystems of the Pechora Sea have a number of hydrological, geological, geomorphological and biological features which distinguish them from other parts of the Barents Sea (Bauch et al., 2005; Nikiforov et al., 2005; Denisenko, 2013; Sukhotin et al., 2019). Key environmental features of the Pechora Sea include:

- Shallow water depths of less than 50 metres for most of the area (with the maximum depth of 210 meters at the Novaya Zemlya trough);
- Significant impact of freshwater continental run-off with up to 80% of riverine input entering the Barents Sea through the Pechora Bay (Kucheruk et al., 2003);
- Mixture of Atlantic water (Kolguev-Pechora current), Arctic water (Litke current), with coastal White Sea and Pechora currents, resulting in highly dynamic water mass characteristics with local temperature and salinity gradients (Gerasimova et al., 2019) and severe seasonal fluctuations of water salinity and temperature (Denisenko, 2013) (Figure 1.2-2);
- Duration of sea ice-cover; almost the entire sea surface for most of the year (October — July), unlike the rest of the Barents Sea that is more impacted by the warm inflow of the Atlantic waters (Dahle et al., 1998; Bauch et al., 2005; Sukhotin et al., 2019);

- Historically low levels of anthropogenic disturbance with no large-scale commercial fisheries happening in the area (Sukhotin et al., 2019).

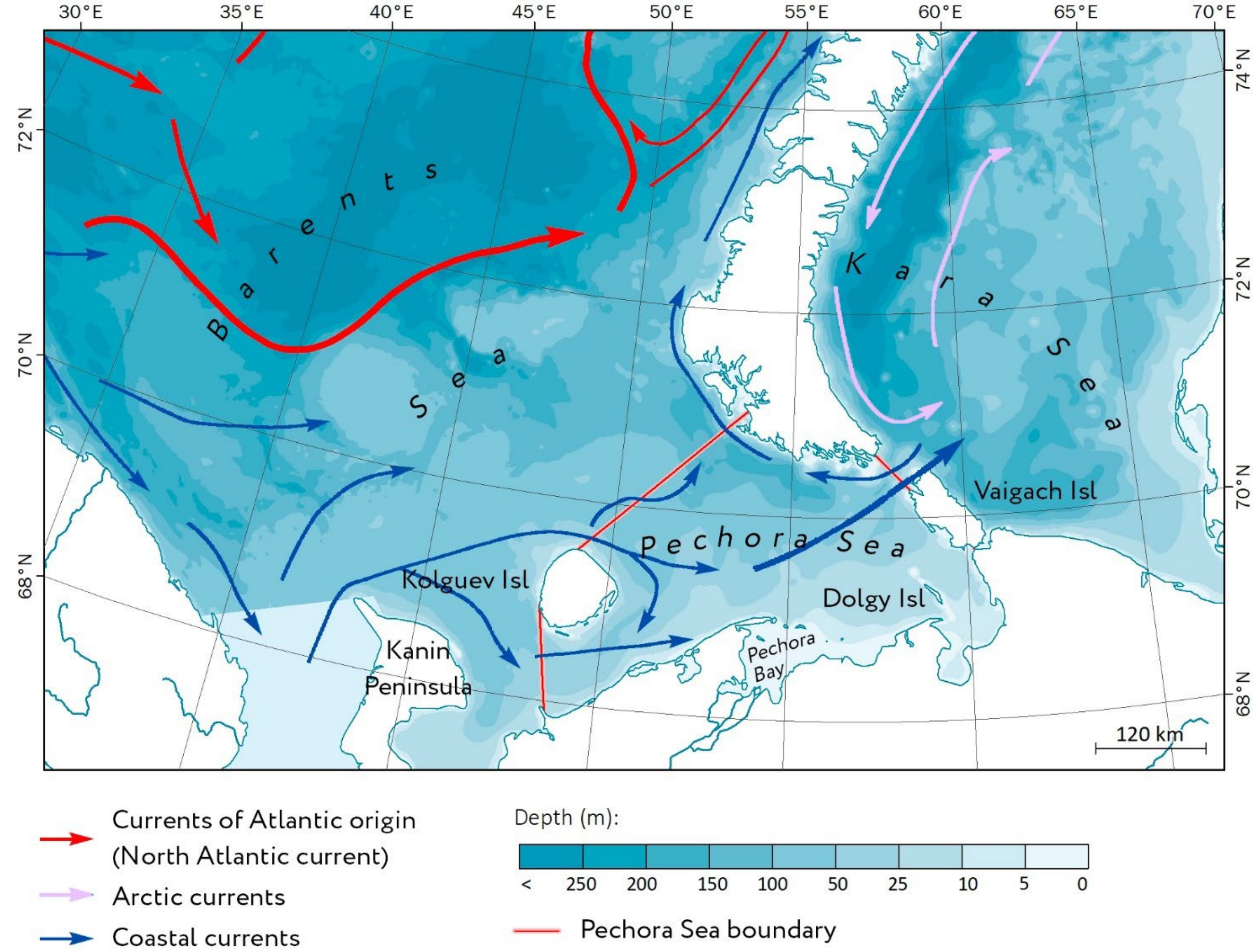


Fig. 1.2 - 2. Geographical boundaries and major currents in the Pechora Sea. Based on the Ecological atlas of the Barents Sea (Shishkin et al., 2020). Map courtesy of the LMSU MRC.

Several areas in the Pechora Sea have recently been selected as components of a network of conservation priority in the Russian Arctic due to their importance as feeding grounds for benthic predators. These include protected species of Atlantic walruses *Odobenus rosmarus rosmarus* (Linnaeus, 1758), nesting and feeding grounds for massive gatherings of benthic feeding waterfowl and stopovers for birds migrating along the East Atlantic flyway (Spiridonov et al., 2017; Sukhotin et al., 2019). Furthermore, the Arctic Marine Shipping Assessment by the Arctic council LMA (PAME, 2009) has identified the entire Pechora Sea as an area of heightened ecological significance in the Barents Sea and listed the following ecological functions as the selection criteria:

- Atlantic walrus wintering area;
- Atlantic walrus feeding and haul-out sites (in summer);

- Moulting and staging areas for waterfowl;
- Moulting and staging area for sea ducks;
- Ringed seal *Pusa hispida* (Schreber, 1775) breeding area (in winter);
- Beluga whales *Delphinapterus leucas* (Pallas, 1776) wintering area;
- Spawning area of polar cod *Boreogadus saida* (Lepechin, 1774);
- Spawning area of Atlantic herring *Clupea harengus* Linnaeus, 1758.

Some researchers refer to the Pechora Sea as one of the most ecologically important areas of the Barents Sea (Larsen et al., 2004). However, our knowledge of the state and dynamics of the Pechora Sea ecosystems remains fragmentary and only recently have systematic ecological monitoring programmes been established, mostly focused on the oil and gas exploration areas.

1.2.2. State of knowledge on the Pechora Sea marine ecosystems

In general, the Pechora Sea ecosystems are less studied compared to the other areas of the Barents Sea. Because of its shallow water depths, complex ice conditions, low productivity and remoteness, the Pechora Sea typically lies outside of the sampling range of the large-scale ecosystem surveys conducted in the Barents Sea (Denisenko, 2013). This is especially true for the benthic surveys that involve seabed sampling as reviewed in Section 1.2.3. Similarly, many ecosystem monitoring programmes in the Barents Sea are linked to the fishery activities and since there are no commercial fisheries in the Pechora Sea, it is often underrepresented in such programmes (e.g., the joint Norwegian-Russian monitoring of the Barents Sea ecosystem programme). It is also important that the Pechora Sea lies solely within the Russian EEZ and is therefore mostly studied by the Russian Academy of Sciences, whereas the majority of bilateral Norwegian-Russian and international research campaigns in the Barents Sea are focused either on the Norwegian waters, or alongside the maritime boundary between Russia and Norway. Recent research activities in the Pechora Sea are typically linked to the oil and gas development, assessment of the status of seabird and walrus populations, or some specific research topics (e.g., hydrodynamics of the water regime in the Pechora Bay). Despite these limitations, some aspects of the Pechora Sea ecosystems are described in the literature in a great level of detail and the following contributions require special acknowledgement:

- *"The Pechora Sea. Outcomes of the integrated studies (physics, hydrology, optics, biology, chemistry, geology, ecology, socio-economic issues"* Edited by Romankevich et al. (2003) [In Russian].

  - This 502-pages book provides likely the most detailed compendium of the outcomes of expeditions conducted in the Pechora Sea in 20th century by the research institutes of the Russian Academy of Sciences and the Russian Federal Service for Hydrometeorology and Environmental Monitoring (Roshydromet). As reflected in the title it covers a broad range of topics from chemistry and hydrology to biology and socio-economic issues.

- *“Pechora Sea Environments: Past, Present and Future”*. Edited by Bauch et al. (2005)
  - This comprehensive volume includes articles on modern environmental conditions, bottom topography, coastal dynamics and morphology, stratigraphy and palaeoceanography, geology and future developments of the Pechora Sea. The latest include modelling sedimentary evolution, and sea-level changes. The volume was developed in a collaboration between Russian, Norwegian and German research institutions.

- “*Biodiversity and bioresources of macrozoobenthos in the Barents Sea. Structure and long-term changes*” by Denisenko, 2013 [In Russian].
  - Most relevant to the focus of this thesis, monography by Sergey Denisenko (2013) provides the first assessment of long-term dynamics of macrobenthic communities in the Barents Sea based on all historical data available from 1920s to 1990s. Chapter 7 reviews macrobenthos of the Pechora Sea.

- *Polar Biology* special issue “*Pechora Sea ecosystems: current state and future challenges*” edited by Sukhotin et al., 2019
  - The special issue on the ecology of the Pechora Sea is comprised of ten research articles looking at zooplankton (Usov et al., 2019), ichthyofauna (Semushin et al., 2019), macrobenthos (Denisenko N. et al., 2019; Denisenko S. et al., 2019), bird communities (Anufriev and Punantsev, 2019), trematodes (Galaktionov et al., 2019), movement patterns and key habitats of Atlantic walruses (Semenova et al., 2019) and POPs in walrus tissues (Boltunov et al., 2019), distribution of bivalve molluscs *Serripes groenlandicus* (Mohr, 1786) and *Macoma calcarea* (Gmelin, 1791) (Gerasimova et al., 2019) and overall current state of the Pechora Sea ecosystems (Sukhotin et al., 2019). The special issue has a prominent focus on the environmental changes observed in the region and effects of climate change on

different elements of marine ecosystems. The authors also highlight that overall state of knowledge of the Pechora Sea ecosystems remains fragmentary and providing baseline data on current state of the Pechora Sea ecosystems is of critical importance as it will enable to determine changes and possible ecosystem shifts in the future (Sukhotin et al., 2019). Papers on macrobenthos included in the special issue are reviewed in more detail in section 1.3 and Chapter 2.

1.2.3. Socio-economic context

The marine ecosystems of the Pechora Sea were, until recently, relatively undisturbed due to scarce coastal population and no significant commercial fisheries in this region unlike most of the Barents Sea (Bauch et al., 2005; Denisenko, 2013). There are no cities on the shores of the Pechora Sea and only a few small historical settlements of fishermen and reindeer herders which are now partly abandoned or repurposed such as the Varandey base camp. Active economic development of the region began in the 1990s when vast offshore oil and gas deposits were discovered, a decade later the *Prirazlomnoye* oil field began production of the Arctic oil and it remains Russia's first offshore oil producing project implemented on the Arctic continental shelf (Sukhotin et al., 2019). *Prirazlomnoye* oil field is in the Pechora Sea approximately 50 km from the protected areas of Vaigach Island (Nature Park) and 30 km from Matveev Island (State Nature Reserve). License for exploration and exploitation of hydrocarbon resources of the *Prirazlomnoye* oil field is owned by Gazprom Neft Shelf (GPNS), a subsidiary of a partially state-owned multinational energy corporation Gazprom. In 2013 GPNS startedoil production operations at the ice-resistant oil-producing stationary platform *Prirazlomnaya*. The platform produced 3.14 million tons of Arctic oil in 2019 with future potential production level estimated as 5.5 million tonnes per year (Gazprom-Neft, 2021). Several additional exploration licenses were issued by the Federal Agency for Mineral Resources in the Pechora Sea, however *Prirazlomnaya* remains the only oil producing project in the Russian Arctic. Locations of the exploration licensed areas and associated ecological monitoring activities are reviewed in section 1.3.2.

In addition to the offshore oil exploration, intensification of shipping in the Northern Sea Route is observed with an average 20% increase per year since 2009 (Miller and Ruiz, 2014), and is projected to continue to grow. Although the Northern Sea Route lies to the east of Novaya Zemlya archipelago with a starting point in the Kara Gate strait, the Pechora Sea is one of the major gateways allowing access to the Northern Sea Route from the continent. The tourism industry has also begun to expand to the Arctic in the recent years with more operators offering cruises to the Barents Sea region including the Pechora Sea. According to the first national ranking of tourism in Russia carried out in 2015, the Novaya Zemlya islands have been listed amongst the top-50 most attractive tourist destinations in Russia (Lukin, 2016).

Anthropogenic pollution is a major threat associated with offshore industries. In the Pechora Sea potential sources of pollution include maritime traffic, continental run-off from the Pechora River, oil and gas exploration, military exercises, and nuclear waste disposal (Sukhotin et al., 2019). However recent assessments have not identified significant contamination in the environment, with negligible levels of average concentrations of organochlorine pesticides, synthetic surfactants, phenols and heavy metals in the Pechora Sea waters (Sukhotin et al., 2019). Despite the ongoing oil production, levels of contamination with oil derivatives (e.g., polycyclic aromatic hydrocarbons (PAHs) and oil films) in the Pechora Sea waters and sediments are below the background values for the Barents Sea (Sukhotin et al., 2019). Furthermore, water pollution with oil films in the Pechora Sea corresponds to the lowest values in the Barents Sea ecoregion (Dahle et al., 2006). Elevated concentrations of radionuclides were reported in sediments and benthic biota in the north-east of the Pechora Sea and are likely associated with the nuclear explosions in Chernaya Bay in the 1950s (Smith et al., 2000). The first study of the persistent organic pollutants in tissues of walruses from the Pechora Sea showed broad individual variation, and compared to data from Svalbard, lower levels of oxychlordane, comparable levels of polybrominated diphenyl ethers (PBDEs), and higher levels of polychlorinated biphenyls (PCBs) (Boltunov et al., 2019). No studies on plastics or microplastics in the Pechora Sea have been published prior to the present study to the extent of the author’s knowledge.

Rapid increases in human activities in the last decades, combined with climate change, striking sea ice retreat, introduction of non-indigenous species and the release of contaminants are predicted to have a strong combined impact on the unique marine ecosystems of the Pechora Sea (Sukhotin et al., 2019; Semenova et al., 2019). Recent assessments of the current state and future challenges of the Pechora Sea ecosystems (Sukhotin et al., 2019) highlighted the importance of biodiversity studies in providing baseline data to underpin future conservation and sustainable management activities in the region.

1.2.4. Oceanographic conditions and climate

Oceanographic conditions of the Pechora Sea are described in a great level of detail in the chapter of the "*Pechora Sea: past, present and future*" volume dedicated to the modern environmental conditions by Nikiforov et al. (2005), and a more recent brief overview is presented in the *Polar Biology* issue by Sukhotin et al. (2019). In the present chapter only the key features of the environmental conditions of the Pechora Sea that are most relevant for the development of benthic fauna are highlighted, whereas a detailed review of the modern and past conditions is outside of the scope of the present work.

Climate

The climate of the Pechora Sea is attributed to high-latitude geographical location and complex hydrological conditions affected by the system of local currents and significant continental run-off. In general, the Pechora Sea is characterised by high variability of hydrometeorological conditions (Gazprom, 2018). Typically, the region has cold winters with significant clouds and low precipitation followed by cool summers with frequent fog and predominantly drizzling rainfall. Air temperature can alternate though the year from -40℃ in winter to +30℃ in summer with an annual average of approximately -5℃ (Nikiforov et al., 2005; Gazprom, 2018).

Ice conditions

Ice conditions are more severe in the Pechora Sea than in the other parts of the Barents Sea LME and the overall ice budget in the Pechora Sea is negative with volume of inflowing through the Kara Gate strait ice higher than the volume of the ice drift discharge (Sukhotin et al., 2019). The Pechora Sea is typically covered with ice from October-November to June-July, although it is never normally fully ice-covered with up to ¼ of the total area remaining free of ice because of the warm Atlantic waters forming an inhibiting ice growth barrier (Nikiforov et al., 2005). Ice cover in the Pechora Sea is typically formed by first-year ice only, the maximum ice thickness is reached in April and the average annual maximum thickness is approximately 90 cm (Mironov et al., 1998; Nikiforov et al., 2005).

Hydrological regime and surface currents

The hydrological regime of the Pechora Sea is determined by interaction of the water masses of the Arctic and Atlantic origin with additional input of continental run-off (Nikiforov et al., 2005; Boltunov et al., 2010; Sukhotin et al., 2019). The local system of currents is described as quasi-stationary circulation formed by the cold Polar waters coming from the Kara Sea with the Litke current, two streams of warm and saline waters of Atlantic origin – Kanin and Kolguev-Pechora currents, and coastal White Sea and Pechora discharge currents.

Table 1.2-1 shows the multiannual average values for sea surface temperature and salinity and bottom water temperature based on Nikiforov et al. (2005). However, recent field studies have demonstrated a consistent increase of sea water temperature in summer, rising from 10.2°C in 2010 to a maximum of 16.8°C in 2013 at 3 m depth near Vaigach Island (Sukhotin et al., 2019).

Table. 1.2 - 1. Hydrological parameters including sea surface and bottom water temperature and salinity based on Nikiforov et al. (2005)**.**

Parameter	**Value according to Nikiforov et al., 2005 (average multiannual data)**		
	Average	Maximum	Minimum
Sea surface temperature, °C	2.8	10.9	-1.8
Bottom water temperature, °C	0	0.8	4.0
Sea surface salinity, ‰	31.55	33.46	12.67

Continental run-off

The Pechora Sea receives approximately 134,000 km^3 of freshwater per year (Dahle et al., 1998). A considerable area of the Pechora Sea is covered by the transition zone where the limnetic waters from the Pechora Bay enter the Arctic Ocean. This transition zone is referred to as “marginal filter” highlighting the importance of biogeochemical transformations, sedimentation and biological processes occurring in the intermixing zone (Usov et al., 2019). The Pechora Sea receives approximately 1,000,000 m^3 of sand and other fractions of sedimentary material as well as 500,000 m^3 of aleuritic-clay matter annually (Dobrovolsky and Zalogin, 1982). Powerful continental run-off from the Pechora River contributes to the beneficial nutrient intake regime for benthic fauna (Boltunov et al., 2010).

Geomorphology and bottom sediments

Seafloor geomorphology of the Pechora Sea represents the main features of its development in the late Pleistocene and Holocene epochs such as the underwater terraces with elongated hollows - the remains of ancient river valleys (Pavlidis et al., 2007). Both at the scale of geological history and in the present day, the continental run-off has a huge influence on the sedimentation, relief formation and hydrological regime of the Pechora Sea, in contrast to the rest of the Barents Sea. Other major factors with an impact on seafloor geomorphology are the ice regime and the coastline permafrost (Pavlidis et al., 2007). Sediments are heterogeneous in the Pechora Sea: well sorted sands prevail in shallow water, silt fractions, aleuritic and pelitic deposits accumulate in the bottom depressions and troughs, silty sands with an admixture of pebbles are concentrated in the central part of the Pechora Sea (Dahle et al., 1998; Sukhotin et al., 2019). The concentration of total organic carbon in sediments varies from 0.1% in continental shelf shallows in the south to 2% in the Novaya Zemlya trough (Sukhotin et al., 2019).

1.3. History of benthic research in the Pechora Sea

1.3.1. Scientific expeditions

Macrobenthic communities of the Pechora Sea have been studied relatively well since the 1920s, with the main research efforts conducted in the 1920s, 1960–1970s, 1990s and in recent years 2016–2020 (Zenkevich, 1927; Brotskaya and Zenkevich, 1939; Antipova, 1973; Dahle et al., 1998; Denisenko et al., 2003; Sukhotin et al., 2008; Denisenko, 2013; Sukhotin et al., 2019; Denisenko N. et al., 2019; Denisenko S. et al., 2019; Gerasimova et al., 2019).

Benthic surveys in the 20th century were carried out by the leading Russian research institutions in marine science and fisheries, namely the Institute of marine fisheries and oceanography of the USSR (IMFO USSR), Murmansk Marine Biological Institute Russian Academy of Sciences (MMBI RAS), Nikolai M. Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Zoological Institute of the Russian Academy of Sciences (ZIN RAS), and Shirshov Institute of Oceanology of the Russian Academy of Sciences (IO RAS). The majority of these expeditions were assessing the entire Barents Sea with only a couple of sampling sites in its south-eastern part, the Pechora Sea. Expedition details for each of the big scientific benthic surveys carried out in the Pechora Sea in 1920–2010s, including research vessels, year of sampling, number of sites, depth range and reference to the published outcomes are provided in Appendix 1-1. Position of the sampling sites (if coordinates were available in the published outcomes of the expeditions) is illustrated in Figure 1.3-1.

Outcomes of the first expeditions in 1924–25 were published a couple of years later in a fundamental research paper by Brotskaya and Zenkevich (1939), that remains a key source of information on benthic habitat mapping of the Barents Sea. The dominant (in terms of biomass) species forming macrobenthic communities of the Pechora Sea were bivalves *Astarte borealis*, *Astarte montagui, Macoma calcarea* (Gmelin, 1791), *Ciliatocardium ciliatum* and *Yoldia hyperborea* (Gould, 1841) and polychaetes *Pectinaria (Cistenides) hyperborea* Malmgren, 1866, and *Maldane sarsi* Malmgren, 1865. Six distinct macrobenthic communities were identified for the entire Barents Sea, two of these communities were in the Pechora Sea and described as follows: “a group of eastern and south-eastern biocoenoses” and “a group of eastern and south-eastern coastal biocoenoses with a significant admixture of Arctic shallow-water forms".

Results of later expeditions by MMBI (1958–1959) and PINRO (1970), despite the large number of sampling sites, did not appear in many papers. Only one relatively short manuscript on distribution of macrobenthos has been published based on the outcomes of the 1970 RV *Nikolay Maslov* expedition by Antipova (1973). Antipova distinguished nine macrobenthic communities in the south-eastern Barents Sea. In addition to bivalve-dominated communities known from before, a new community characterised by sea urchin *Strongylocentrotus* and barnacle *Balanus* was described south of the Novaya Zemlya Islands (Antipova, 1973). RV *Professor Derugin* expeditions by MMBI resulted in a few short publications mostly focused on different groups of invertebrates (e.g., bivalve molluscs - Galkin, 1964; Galkin, 1998; polychaetes - Streltzov, 1966), but the overall results of the expedition have not been published.

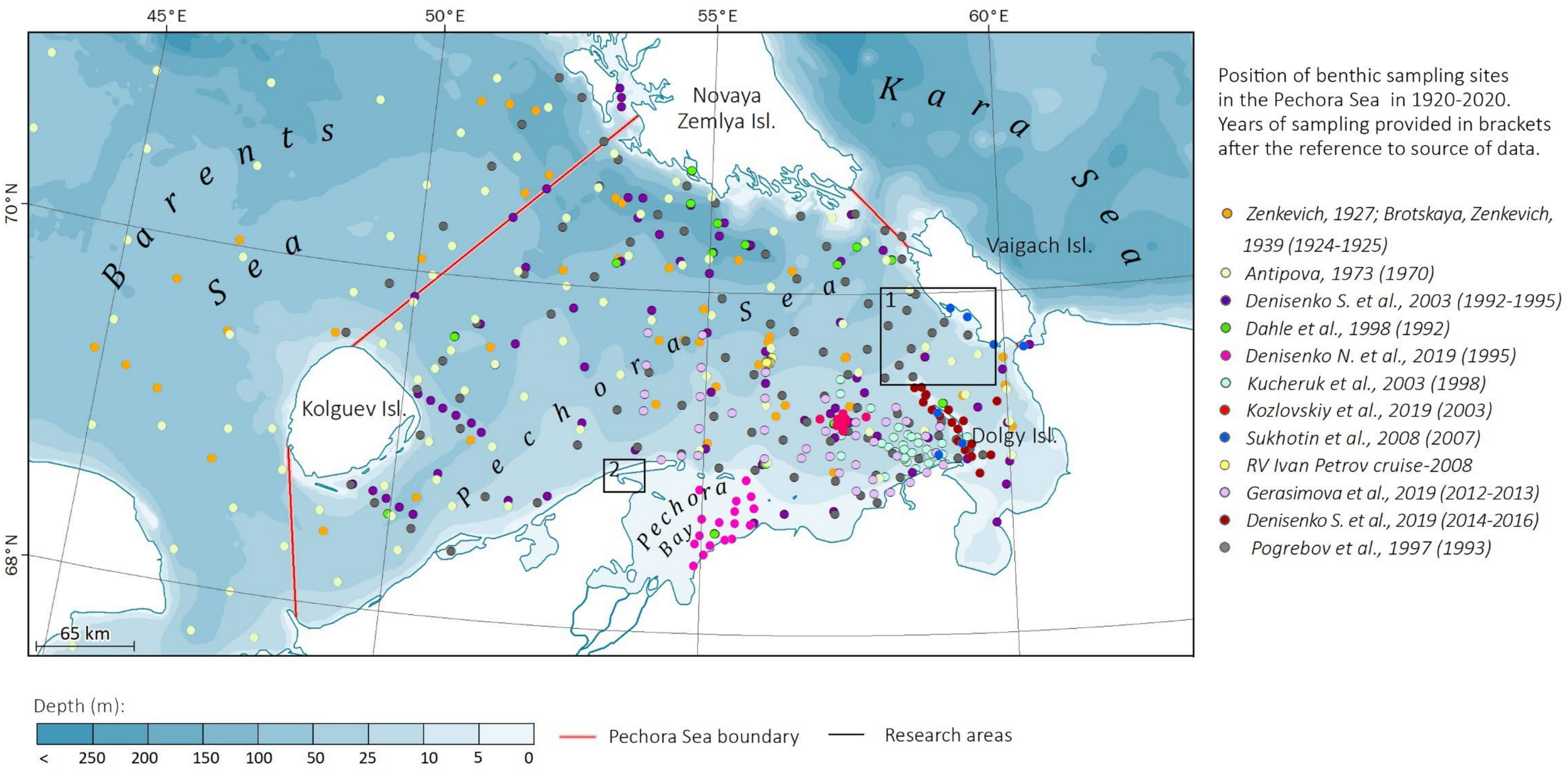
In 1990s discovery of oil and gas-bearing structures in the Barents Sea attracted special attention to the region, in particular to the *Prirazlomnoye* oil field in the central part of the Pechora Sea. In 1993 a large survey of 112 sites was conducted in the area of the oil field, resulting in a short summary paper published several years later (Pogrebov et al., 1997). Another survey with a focus on shallow water communities near Dolgy Island and future location of the Prirazlomnoya oil platform (5–28 m water depth range) was conducted by IO RAS onboard RV *Akademik Sergey Vavilov* in 1998, at 37 sampling sites (Kucheruk et al., 2003). Ecological monitoring within the oil field is reviewed below in Section 1.3.2.

In 2013, Stanislav Denisenko reviewed all historic data available including archive materials by MMBI and PINRO and his own field data collected in 1991–1995 (Dahle et al., 1998; Denisenko et al., 2003) and in his extensive monography on structure and long-term dynamics of macrobenthos of the Barents Sea (Denisenko, 2013). To date this book provides the most comprehensive review of all benthic data collected prior to 1995.

Notably, historical data on macrobenthos of the Pechora Sea (including monography by Denisenko, 2013) are predominantly only available in the Russian language. Manuscripts by Pogrebov et al. (1997), Dahle et al. (1998) and Denisenko et al. (2003) were the first scientific publications on macrobenthos of the Pechora Sea in English.

The latest studies in the 21st century were often of a smaller scale and were focused on small areas of the Pechora Sea with specific goals, e.g., description of the estuarine communities of the Pechora Bay (Denisenko N. et al., 2019); assessment of biota associated with blue mussels near Dolgy Island (Sukhotion et al., 2008), or evaluating benthic foraging resources of Atlantic walrus near Dolgy Island (Denisenko S. et al., 2019). Macrozoobenthos of the central and northern parts of Pechora estuary were discussed in a recent publication by Denisenko N. et al. (2019). The authors sampled twenty estuarine sites in the Pechora Bay during the RV *Geophysic* expedition in spring 1995 and compared the Pechora Bay macrozoobenthos with that of the Ob Bay in the Kara Sea (Denisenko et al., 1999). This paper was featured in a recent special issue of *Polar Biology* dedicated to the current state of the Pechora Sea ecosystems, led by Sukhotin, Denisenko and Galaktionov (2019). The issue also featured articles by Gerasimova et al. (2019) on distribution of *S. groenlandicus* and *M. calcarea* (data collected in 2012–2013); and by S. Denisenko et al. (2019) on macrobenthos near the walrus haul-out sites on Dolgy and Matveev Islands (data collected in 2014 and 2016).

Aside from the scientific research expeditions, since the beginning of the active oil exploration and production in the Pechora Sea (early 2000s), the area has been extensively studied by the oil and gas companies with regular ecological monitoring surveys within the exploration areas. Information related to ecological monitoring programmes is reviewed in Section 1.3.2.



Position of sampling sites of the benthic surveys in the Pechora Sea since the 1920s. Map courtesy of the LMSU MRC.

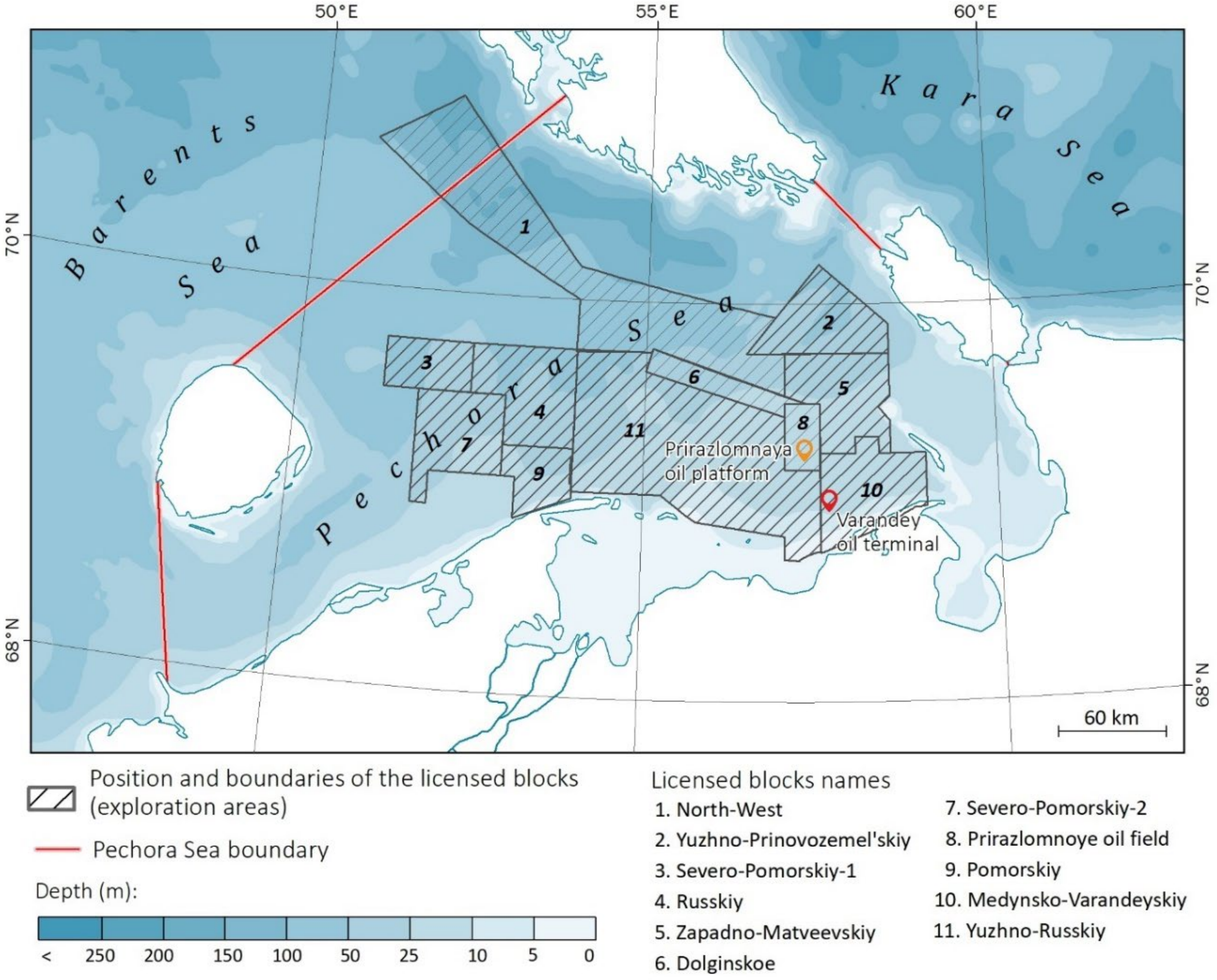
1.3.2. Ongoing ecological monitoring

The Barents Sea is an area of strategic economic interests of the Russian Federation because it contains vast hydrocarbon reserves, and the Pechora Sea is of particular importance as it is the location for one of the largest and the only offshore oil producing field in the Russian Arctic shelf, the *Prirazlomnoye* oil field. Prior to the construction of the *Prirazlomnaya* platform, a programme of ecological monitoring of the Pechora Sea ecosystems had been developed and accepted ensuring environmental impact assessment and environmental monitoring thereinafter during all stages of operations at the platform (Gazprom, 2018). Monitoring has been carried out annually since 2010 at 10 sites and includes meteorological measurements, oceanographic profiling, hydrogeochemical, geological and biological sampling, water and air quality control, alongside marine mammal and bird observations. In addition to ecological monitoring, GPNS carries out a special programme on conservation of Atlantic walruses in the Pechora Sea since 2013, and a biodiversity conservation programme since 2015 (Gazprom, 2018).

Full ecological monitoring reports are confidential and not available for public access, however, short summaries for each of the recent years are published on the official GPNS website (GPNS, 2015; GPNS, 2016; GPNS, 2017). In addition, in 2018 GPNS published an ecological atlas of the Pechora Sea with a brief review and synthesis of ecological surveys conducted by the company in 2010–2017 and general characteristics of different components of marine ecosystems, including macrobenthos (Gazprom, 2018). Brief reports describe macrobenthos near the platform as a barren community of 76 species with mean biomass (wet mass) of approximately 20 g/m^2 and overall dominance of *S. groenlandicus* (GPNS, 2017). It is also noted by the latest report that at some sampling sites bivalve molluscs and ascidians have been replaced in the recent years by smaller organisms including polychaetes and bryozoans, which has been linked to increasing numbers of a mobile benthic omnivore, the snow crab in the area (GPNS, 2017).

Whereas the *Prirazlomnoye* oil field remains the only oil producing project in the Pechora Sea and in the entire Russian Arctic continental shelf, multiple exploration licenses have been issued in the Pechora Sea by the Federal Agency for Mineral Resources, covering approximately half of the entire water territory of the sea (Figure 1.3-2). Two more exploration licenses are held by *Gazpromneft*, namely, *North-West* (*Severo-Zapadny*) licensed block and *Dolginskoye* oil field (Gazprom-Neft, 2021). Another eight licenses are owned by *Rosneft,* another one of Russia’s leading oil companies, and the largest in terms of shelf assets (Rosneft, 2021). The licensed blocks owned by *Rosneft* are located in the central, western and southern parts of the Pechora Sea, surrounding *Prirazlomnoye* oil field (Figure 1.3-2).

Geological surveys and other operations in the licensed blocks are typically supported by background ecological monitoring as a part of license agreements. Details of all operations in the licensed blocks are stored in the archives of the Russian Federal Geological Fund (Rosgeolfond), however the reports from those monitoring programmes are not accessible for public use. No data on macrobenthos in the Pechora Sea obtained during operations on the licensed blocks have been published as open access with the exception of reports featuring macrobenthos of the *Prirazlomnoye* oil field.



1.4. Conservation status of the Pechora Sea

Environmental protection in Russia is regulated by the Federal Law “On environmental protection” (№ 7 FZ of January 10, 2002, see FZ 7 (2002)), with protected areas defined in Federal Law “On protected areas” (№ 33 FZ of February 15, 1995, see FZ 33 (1995)). According to FZ-33, protected areas can have federal, regional, or local status of significance. At the same time, according to Russian legislation, all internal water territories inside the exclusive economic zone (EEZ) are subject to federal jurisdiction, which results in all marine protected areas (MPAs) having federal status such that they can only be altered at the federal level (Spiridonov et al., 2020).

In Russian legislation, protected areas include (1) Zapovedniks (State nature reserves including State biosphere reserves); (2) National parks; (3) Nature parks; (4) State nature zakazniks (protected areas more accessible than zapovedniks); (4) Natural monuments; (5) Dendrological parks and botanical gardens. Zapovedniks have the highest degree of environmental protection enforcement (IUCN category 1) with no economic use of land allowed and strict restrictions on public access. There are 103 zapovedniks in Russia (Ministry of Nature Resources, 2021), of which only 5 have marine components and only one expands to the Pechora Sea, that is the Nenetsky Zapovednik (State Nature Reserve).

1.4.1. Summary of the current conservation status of marine ecosystems of the Pechora Sea

The Arctic Council has carried out work to identify areas of heightened ecological significance within the 16 Large Marine Ecosystems of the Arctic region under the Arctic Marine Shipping Assessment (PAME, 2009). Identified areas of heightened ecological significance comprise a total area of 12 million km^2 (AMAP/CAFF/SDWG, 2013). This report assessed ecological functions in different regions and extent to which these areas corresponded to an ecological criteria of particularly sensitive sea areas established by the international maritime organisation (IMO). Notably, assessed ecological functions relate mostly to marine mammals, birds and fish, whereas little consideration was given to other groups of marine biota, including benthic invertebrates.

The south-eastern Barents Sea encompassing entire water territories of the Pechora Sea was designated as an Ecologically and Biologically Significant marine Areas (EBSA) having been nominated by the Arctic Council in 2013 (AMAP/CAFF/SDWG, 2013) following the Arctic Marine Shipping Assessment in 2009 (PAME, 2009). The area met multiple EBSA criteria due to their importance as (1) spawning areas for the polar cod *B. saida*; (2) breeding areas of ringed seals *P.*

hispida near the Kanin peninsula; (3) summer haul-outs of the Atlantic walruses *O. rosmarus rosmarus* near Vaigach Island; (4) moulting and staging areas for geese (dark-bellied brent goose *Branta bernicla* (Linnaeus, 1758), barnacle goose *Branta leucopsis* (Bechstein, 1803), and others); (5) moulting and staging areas of sea ducks (AMAP/CAFF/SDWG, 2013).

A total of 15–19 species of marine mammals and numerous waterfowl species can be observed in the Pechora Sea in different seasons (Sukhotin et al., 2019), but the largest gatherings are formed by the Atlantic walruses (summer haul-outs of 2000–4000 individuals - Lydersen et al., 2012; Semenova et al., 2019) and sea ducks (gatherings of hundreds of thousands of individuals predominantly formed by the King eiders *Somateria spectabilis* (Linnaeus, 1758) and the common scoters *Melanitta nigra* (Linnaeus, 1758) (Sukhotin et al., 2008). Atlantic walruses, King eiders and macrobenthic communities are all listed as focal ecosystem components (FECs) under the Circumpolar Biodiversity Management Program (CBMP) by the Conservation of Arctic Flora and Fauna working group (CAFF) of the Arctic Council (CAFF, 2017). Macrobenthic communities have an integral role in marine ecosystems of the Pechora Sea as they constitute foraging grounds sustaining populations of benthic predators including Atlantic walrus *O. rosmarus rosmarus*, King eider *S. spectabilis*, bearded seal *Erignathus barbatus* Erxleben, 1777, common eider *Somateria mollissima* (Linnaeus, 1758), common scoter *M. nigra*, velvet scoter *Melanitta fusca* (Linnaeus, 1758), long-tailed duck *Clangula hyemalis* (Linnaeus, 1758), snow crab *C. opilio*, great spider crab *H. araneus* and hermit crab *P. pubescens*. However, the framework of marine protected areas currently existing within the Russian zone of the Barents Sea does not consider the state of macrobenthos. Furthermore, the protected area established on Vaigach Island is to safeguard key haul-out and breeding sites of bird species and does not extend to nearby water territories that contain key foraging grounds of both walruses and waterfowl. Therefore, understanding of the state and dynamics of benthic ecosystems in the foraging grounds of benthic predators is vital to improving the marine spatial planning in the area.

1.4.2. Nature conservation regimes in the research areas

Nature conservation regimes are different in the two research areas – Pechora Bay and Vaigach Island. Pechora Bay and Matveev Island lie within the water territory of the Nenetsky State Nature Reserve, while Vaigach Island is partly covered by Vaigach Nature Park, but the borders of the park do not extend to the nearby water territory (Figure 1.4-1). The entire Pechora Sea is classified as EBSA by the Arctic Council’s Arctic Marine Shipping Assessment due to its importance as a spawning area for Atlantic herring and polar cod, feeding and haul-out areas for Atlantic walruses, and moulting and staging areas for waterfowl (AMAP/CAFF/SDWG, 2013). However, at present only a small proportion of the total area belongs within the protected areas of the Nenetsky State Nature Reserve, and the rest of the sea is not protected.

The Nenetsky State Nature Reserve was established in 1997 to safeguard important foraging grounds for marine ducks, including the King eider and the common scoter from rapidly developing industrial activities in the region. Both species together use Dolgy Island to feed and moult before migrating to wintering grounds (Sukhotin et al., 2008). The main aim of establishing the nature reserve was the protection of important habitats for waterfowl that stopover in shallow waters of the Pechora Sea during their migration from reproduction sites in West Siberia to variable wintering sites (Sukhotin et al., 2008). The Nenetsky Nature Reserve provides nesting and feeding grounds, and forms part of the migration routes for 125 species of waterfowl and coastal birds. This includes species from the red list of endangered species of the Russian Federation and IUCN red list of threatened species, such as: the yellow billed loon *Gavia adamsii* (Gray, 1859); Bewick's swan *Cygnus columbianus bewickii* (Yarrell, 1830); the lesser white-fronted goose *Anser erythropus* (Linnaeus, 1758); the red-breasted goose *Branta ruficollis* (Pallas, 1769) and others (IUCN, 2021).

Foraging macrobenthos were studied near the coasts of Dolgy Island (Sukhotin et al., 2008; Denisenko S. et al., 2019), but also to a lesser extent in other parts of the Pechora Sea. Mismatch between ornithological and macrobenthic data for the region has been previously noted by Sukhotin et al. (2008). The Nenetsky State Nature Reserve covers the Pechora River estuary and nearby islands. In total the reserve covers an area of 313,400 hectares of which more than a half (181,900 hectares) corresponds to marine areas (Nenetsky Zapovednik, 2021).

Vaigach Island is also classified as a protected area (Nature Park); however, Nature Park provides a lower level of protection compared to the State Nature Reserve in Russian legislation, which is why the protected areas of Vaigach Nature Park cannot extend to the nearby water territories. Figure 1.4-1 illustrates the layout of the protected areas of national and regional level near the research areas in the Pechora Sea.

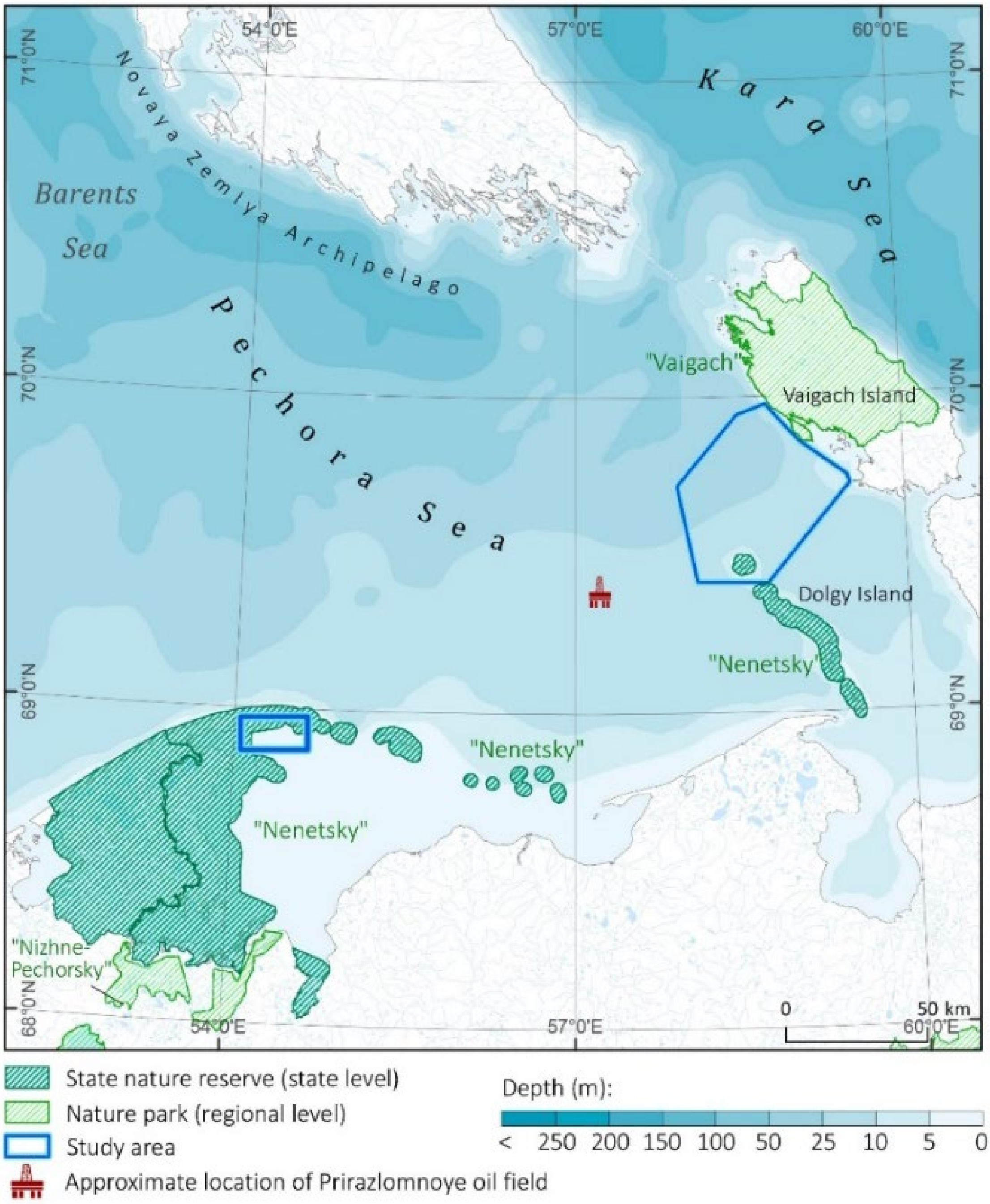


Fig. 1.4 - 1. Protected areas of national and regional level near the research areas in the Pechora Sea. Light green dashing indicates borders of the Vaigach Nature Park (regional level); dark green dashing shows territory of the Nenetsky State Reserve. Blue polygons represent sampling areas. Map courtesy of the LMSU MRC.

1.5. Summary

The Pechora Sea in the Russian Arctic is recognised as an Ecologically and Biologically Significant marine Area by the Arctic Council (AMAP/CAFF/SDWG, 2013) due to the important spawning areas of fish, breeding areas of marine mammals, summer haul-outs of the Atlantic walruses and moulting areas of different bird species that it contains. Many of the protected species in the Pechora Sea are benthic predators, however the existing layout of the marine protected areas does not extend to the foraging areas of these species. Monitoring of the state and dynamics of benthic communities is critically important for improving the management of marine protected areas in the region. Despite the long observation history reviewed in Sections 1.2 and 1.3., there are still very considerable knowledge gaps in the understanding of benthic biodiversity in the Pechora Sea, and especially in the shallow-water areas.

Marine biodiversity of the Pechora Sea is impacted by multiple stressors present in the region and reviewed in Section 1.1. It is outside of the scope of this thesis to identify the level of impact of each of these stressors on the biodiversity of the Pechora Sea; however, each of the following Data Chapters introduces in more detail stressors that are mostly relevant to the studied aspects of benthic ecosystems and biodiversity. Thus, climate change and more specifically dynamics of climate index of the Barents Sea (an approximation of mean values of air temperature, water temperature and ice-free area normalised by standard deviations following Boitsov et al., 2012) are introduced in Chapter 2. Chapter 3 focuses on regional non-indigenous species; Chapter 4 addresses marine plastic and microplastic pollution; and Chapter 5 consolidates a list of suggested drivers of environmental change that have an impact on a regional scale on benthic ecosystems and biodiversity of the Pechora Sea.

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Chapter 2. The current state and interannual variability of macrobenthic communities in the Pechora Sea

Chapter focus

Chapter 2 investigates the current state and interannual variability of macrobenthic communities in the Pechora Sea through analyses of field data from the two research areas: (1) the foraging grounds of Atlantic walrus near Vaigach Island; (2) the shallows of Pechora Bay in the Nenets State Nature Reserve. Potential drivers of change in macrobenthos are reviewed in the Discussion. The chapter begins with a literature review discussing ecological theories explaining temporal change in macrobenthos and why macrobenthos are used in environmental monitoring.

2.1. Abstract

Macrobenthic communities of the Pechora Sea form foraging grounds vital for sustaining apex predators including the keystone protected species Atlantic walrus. Benthic surveys have been conducted in the Pechora Sea since the 1920s, however, there is a paucity of data on shallow water communities and a lack of understanding of temporal variability of macrobenthos. These gaps are compounded by a lack of systematic approaches to data collection with sampling gear, research areas, and data interpretation. This chapter aimed to address these gaps by characterising current state and interannual variability of the underrepresented shallow-water benthic communities in the Pechora Sea.

Samples of macrobenthos studied in this chapter were collected during the field campaigns in the Pechora Sea in 2015–2020 from the two research areas: (1) shallows of the Pechora Bay within the Nenetsky Nature Reserve water territories, where the first description of shallow water communities in the margins of their distribution was conducted; (2) foraging grounds of Atlantic walrus near Vaigach Island (these rich in biomass grounds were assessed to characterise available macrobenthic resources in 2016, and then assessed for interannual variability based on the additional samples obtained in the following years).

A macrobenthic community dominated by *Limecola balthica* with a wet biomass of 21.31±0.32 g/m^2 and 14 species in total was recorded in the Pechora Bay. The community is comprised of eurythermal and euryhaline species and is reduced in biomass compared to *L. balthica*-community described for the central part of the Pechora Bay (Denisenko N. et al., 2019). Paucity of macrozoobenthos in the area is attributed to extreme environmental conditions

including freezing of the water column to the bottom during winter and reduced salinity caused by under-ice spread of the freshwater flow.

Near Vaigach Island a heterogeneous macrobenthic community of 184 taxa (148 identified to species level) with mean biomass of 222.06±229.02 g/m^2 was described. Bivalve molluscs, particularly *Astarte borealis*, *Ciliatocardium ciliatum* and *Astarte montagui,* dominated the overall macrobenthic biomass making two-thirds of it. During the six years of sampling, mean biomass, abundance, relative production, and species composition fluctuated with no clear trends between the years. Observed differences were attributed to high heterogeneity of macrobenthos and varying dominant and subdominant species on each sampling site (four different sub-communities have been identified within the research area). The fluctuation period of the climate index in the Barents Sea is estimated as 25–30 years, therefore longer data series are needed to detect climate-induced shifts in benthic communities. At present, long-term cumulative impacts from environmental change, biological interactions and anthropogenic pressures on macrobenthos in the Pechora Sea remain uncertain. Long-term ecological monitoring with a consistent framework for data collection and interpretation is needed to effectively detect and predict changes in benthic communities. Biomass of key prey items, including *A. borealis*, *C. ciliatum* and *A. montagui* can be used as an indicator parameter of foraging capacity of the area in future studies.

2.2. Introduction

Benthic ecosystems of the Pechora Sea are typically characterised by shallow water depths, low temperatures of near-bottom water, predominance of silty sands in the bottom sediments, and a high spatial heterogeneity of benthic communities ranging from barren communities with extremely low biomass and biodiversity, to particularly high biomass overwhelmingly dominated by bivalve molluscs (Antipova, 1973; Denisenko, 2013; Sukhotin et al., 2019). The first observations of macrobenthos in the Pechora Sea were conducted in the 1920s (Zenkevich, 1927; Brotskaya and Zenkevich, 1939) followed by several large benthic expeditions in the second half of the 20th century (1950–1970s), and several smaller surveys from the early 1990s and thereafter. In addition to scientific expeditions, regular ecological monitoring surveys conducted by oil and gas sector in the recent years (since the mid-2000s) gather valuable data on the state of marine ecosystems, including macrobenthos. A review of the history of benthic observations in the Pechora Sea is presented in the Introduction chapter of this thesis. However, despite the relatively long history of benthic research in the area, the data on macrobenthic communities remain sporadic with some areas particularly underrepresented. Understanding of the state and dynamics of benthic assemblages provides valuable insights on the state and health of marine ecosystems, and allows early detection of potential ecosystem shifts, which is why monitoring of macrobenthos is essential for sustainable management of marine resources.

In this Chapter, I review the state of knowledge on macrobenthos of the Pechora Sea, identify knowledge gaps, and provide new data addressing these knowledge gaps, looking at the current state and interannual variability of macrobenthic communities near Vaigach Island and in the Pechora Bay.

2.2.1. Why and how are macrobenthic communities used in ecological monitoring?

Brief introduction to key ecological theories explaining temporal change in macrobenthos.

Ecological monitoring of macrobenthos

Seafloor fauna are characterised as the most conservative biotic component of marine ecosystems – as opposed to plankton and pelagic species, benthic communities are typically dominated by infaunal long-living species that are spatially stable and less affected by seasonal and temporal fluctuations in environmental conditions (Clark and Frid, 2001; Mokievsky and Tzetlin, 2020). In addition, infaunal benthic communities are useful for studies of local effects of pollutants (Clarke and Warwick, 2001). Benthic communities are broadly used in environmental monitoring as indicators of the state of marine ecosystems. For example, under the European Water Framework Directive (MSFD; 2000/60/EC) metrics of benthic communities included in the assessment of ecological status of ecosystems include diversity and abundance of invertebrate taxa, and the proportion of disturbance-sensitive taxa (Borja et al., 2009). It is important to clarify, that community dynamics of invertebrate taxa differ between the size classes of organisms (micro-meio- and macrobenthos). Typically, in ecological monitoring only macrobenthos retained by a 1.0-mm-mesh sieve are sampled due to longer life spans of dominant species and established sampling techniques (Mokievsky and Tzetlin, 2020), and therefore this chapter only focuses on macrobenthos.

One of the fundamental questions in benthic ecology is how to distinguish between human-induced shifts in macrobenthos and natural variability in the structure of benthic communities (Borja et al., 2009). Natural variation in benthic communities can be attributed to long-term trends, or aperiodic shifts, however, to what extent this change can be forced by anthropogenic pressures, including direct impacts from offshore industries and human-induced change in environmental conditions including climate change, ocean acidification, marine pollution and introduction of non-indigenous species remain unresolved (Frid, 2011; Clare et al., 2015; Mokievsky and Tzetlin, 2020).

Under the Circumpolar Biodiversity Monitoring Programme (CBMP) macrobenthic communities are classified as focal ecosystem components, central to functioning of ecosystems, and recommended for monitoring as proxies of change in the environment (CAFF, 2017).

Long-term ecological research

Long-term ecological research (LTER) provides means to detect changes in the structure of the communities that are less affected by seasonal and temporal fluctuations of oceanographic conditions (Mokievsky and Tzetlin, 2020). Consistent sampling and identification of macrobenthos requires significant research efforts and our understanding of long-term trends in macrobenthos is limited to long-term data series available that remain fragmented and sporadic. The need for long-term observations is recognised globally, leading to establishment of coordinated ocean observation networks with a purpose of integrating global observations and addressing challenges imposed by growing anthropogenic pressure (Muelbert et al., 2019).

Examples of LTER systems include the International Long-Term Ecological Research Network (ILTER), Ocean Observatories Initiative (OOI), Distributed Biological Observatory (DBO) and regional networks of the Global Ocean Observing System (GOOS). However, the integrated ocean observation systems are predominantly comprised by autonomous data collection equipment and registration of oceanographic variables, whilst systematic collection of biological samples is more complicated and currently lacking from most LTER systems. In the Arctic region, the deep-sea observatory HAUSGARTEN established by the German Alfred Wegener Institute for Polar and Marine Research (AWI) in Fram Strait in 1999 remains the only polar LTER observatory providing data on macrobenthic invertebrates (Soltwedel et al., 2005).

Temporal change and regime shifts

Dynamics of macrobenthic communities can be pronounced in changes of species composition, abundance, biomass and other parameters. Various terminology is used in literature to characterise the change, including stochastic fluctuations, oscillations, regime shifts, long-term trends, successions, periodic and aperiodic shifts, noise, etc (Lees et al., 2006; Frid, 2011). Recent classification by Mokievsky and Tzetlin (2020) divides variety of trends into the following types of dynamics of benthic assemblages:

- Self-oscillatory processes (stochastic or periodic fluctuations in parameters of macrobenthos).
- Periodic and quasi periodic shifts (significant change in community structure, resulting in different community, e.g., succession of communities on hard substrates and fouling communities)

- Aperiodic shifts induced by external factors:
    - Community shifts induced by edificatory species (including introduction of non-indigenous species).
    - Regime shifts induced by transformation of habitats (e.g., coastal erosion caused by permafrost thaw; eutrophication; desalination).

Regime shifts in the marine environment are defined as abrupt changes in ecosystems that occur in physical and ecological components of ecosystem concurrently, observed through several trophic levels and are especially pronounced in biological variables, also described as low frequency, high-amplitude changes (Lees et al., 2006). Classification of regime shifts by Collie et al. (2004) includes three types: (1) smooth regime shifts (where relationship between the forcing and response variables is quasi-linear); (2) abrupt regime shifts (where forcing and response variable have a non-linear relationship); (3) discontinuous regime shifts (where the response variable transitions between unstable equilibrium of several states). In theory, all described patterns of community changes and regime shifts can be observed in macrobenthic data, although in practice these patterns are often not readily apparent from inspection of data (Clarke and Warwick, 2001).

Ecological regime shifts are often associated with dramatic biodiversity loss. Some examples include severe degradation of marine ecosystems, for example of the Black Sea associated with overfishing and jellyfish blooms (Daskalov, 2002), or habitat destruction and benthic biodiversity loss in the Barents Sea as result of the invasion of the red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Falk-Petersen et al., 2011). Numerous other examples of regime shifts occurred in the North Atlantic, North Pacific, Jamaica, California, Baltic Sea and other areas (reviewed in Lees et al., 2006), and were likely associated with climatic regime shifts, or over-exploitation of marine resources. Therefore, early detection of changes in marine ecosystems is crucial for attempts at sustainable management of marine resources and conservation of biodiversity. Characteristics of macrobenthic fauna can be subject to both top-down control by benthic predators and bottom-up control by the lower trophic level. Therefore, changes detected in macrobenthic communities that are more spatially and temporally stable and therefore suitable for monitoring can reflect changes occurring in other trophic levels and ecosystem as whole (Harvey et al., 2003). For example, in the North Sea biological linkages between benthic and pelagic communities were revealed through observations of climate-induced changes in plankton (Kirby et al., 2007).

Resilience of benthic communities

A key concept describing ecosystem response to disturbance is resilience. Resilience is the ability to resist and recover from external disturbances or perturbations (Dayton, 1972). It is important to distinguish between resilience and stability, where the latest is consistency of mean values of indicator parameters over time (Dayton, 1972), applied to macrobenthic assemblages this can mean stability of species composition (including dominant species), abundances and biomass. Gollner et al. (2017) uses the following characteristics to describe resilience of marine ecosystems:

- *Resistance*. Characteristic that shows how much impact ecosystem can absorb before its condition begin to change.
- *Reversibility*. Characteristic of whether an ecosystem can return to a state where it was before the impacts of disturbance events began.
- *Recovery*. The rate at which ecosystem can return to a pre-disturbance condition.

Resilience of benthic communities to alterations has been studied in a context of bottom trawling (Collie et al., 1997; Gray et al., 2006; Eigaard et al., 2016; Rijnsdorp et al., 2016; Hiddink et al., 2017; Clark et al., 2019), and more recently with respect to deep-sea mining (reviewed in Gollner et al., 2017). The tendency for both resistance and recovery vary greatly amongst individual macrobenthic species, some of which are more sensitive to environmental conditions than others (Gollner et al., 2017). However, as assemblages, macrobenthos can demonstrate high long-term resilience due to species substitutions that allow maintenance of ecological functioning of the benthic ecosystem, this effect is known as an “insurance hypothesis” (Frid, 2011).

The Arctic benthic fauna is comprised by a variety of species with different levels of tolerance to changes in temperature and salinity. It has been shown that temperature tolerance is a conservative trait (Hirche et al., 1997). Arctic Biodiversity Assessment (ABA) conducted by the Conservation of Arctic Flora and Fauna (CAFF) working group of the Arctic Council states that one of the temporal trends observed in the Arctic based on the limited time-series data available is borealization of fauna (both benthic and pelagic) in the Arctic marginal seas (CAFF, 2013). It is predicted that ongoing climate change will lead to shifts in species distributions, potential Pacific-Atlantic trans-Arctic interchange of species and related loss of endemic Arctic biodiversity (CAFF, 2013). However, cumulative effects of climate change and anthropogenic activities on resilience of Arctic benthic communities are unknown and although out of the scope of this study, understanding of a threshold passing which benthic ecosystems are unlikely to recover, is crucial for sustainable future of the Arctic marine ecosystems.

Methodological approach to statistical analysis

To detect changes in benthic communities, time series data are used, which are usually arranged in species-by-samples arrays and inspected by statistical testing to identify and characterise temporal and spatial variability of community structure (Clarke and Warwick, 2001). Most common statistical techniques used to characterise benthic communities and their variability can be divided into (1) univariate methods (diversity indices, indicator species); (2) distributional techniques (k-dominance curves, species accumulation curves, abundance-biomass comparison (ABC) curves, species distribution models); and (3) multivariate methods (hierarchical clustering, non-metric multidimensional scaling (nMDS), principal component analysis (PCA)) (Clarke and Warwick, 2001). Multiple analysis of variance (MANOVA) or nonparametric analogues (e.g., PERMANOVA) are commonly used to assess contribution of variables (year of sampling, geographical coordinates, water depth, etc) to dynamics of analysed variable (e.g., mean abundance of macrobenthos) (Azovsky, 2019).

One of the crucial questions when choosing methodological approach is which attributes or parameters of macrobenthos are the most ecologically meaningful. Typically, data from benthic surveys include information on abundance and biomass of each identified species in each sample. Abundance data are commonly used in environmental impact assessments (Clarke and Warwick, 2001). However, it is shown, that for soft-sediment benthic communities biomass data are a better measure of the relative ecological importance (Clarke and Warwick, 2001). In addition, “relative production” approximated as a relationship between biomass and abundance is commonly used 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., holothurians, large gastropod or bivalve molluscs, and decapod crustaceans). Clarke and Warwick (2001) suggest the following calculation of relative production:

$$\mathrm{P}=(B/A)^{0.73}\times A$$

Where B refers to biomass, A refers to abundance, 0.73 refers to the average exponent of annual relative production on body-size for macrobenthic invertebrates (Clarke and Warwick, 2001). Some researchers add coefficient k to this formula that approximates metabolism intensity in different groups (reviewed in Mokievsky et al., 2012).

In the present work an integrated approach was used, and all three attributes (biomass, abundance and productivity) were assessed with a combination of distributional and multivariate methods (see Methods section of this chapter for a full list of statistical tests used).

2.2.2. Current state of macrobenthos in the Pechora Sea

There are 712 macrobenthic invertebrate taxa recorded in the Pechora Sea according to the most comprehensive review by Denisenko (2013), representing approximately 35% of the benthic species richness of the entire Barents Sea. Most diverse groups of organisms in terms of species richness are polychaetes, crustaceans and molluscs, with bivalve molluscs contributing the most to overall biomass (Brotskaya and Zenkevich, 1939; Antipova, 1973; Kucheruk et al., 2003; Denisenko et al., 2003). Benthic fauna of the Pechora Sea is mostly comprised of boreal-Arctic (approximately 60%) and Arctic species (approximately 30%) with a limnetic signature due to inputs from the Pechora River estuary (Antipova, 1973; Denisenko, 2013).

Compared to the rest of the Barents Sea, macrobenthos of the Pechora Sea are characterised by a relatively high faunal diversity and high variability in spatial distribution and in biomass, presumably due to local environmental heterogeneity in seafloor topography and sediment type (Dahle et al., 1998; Denisenko et al., 2003). Paucity of macrobenthos (both in terms of biomass and biodiversity) is typical for the silty sands in the shallow waters of sublittoral areas. This is especially the case in the areas influenced by freshwater continental run-off such as silty-sandy-ooze in the Pechora Bay and Khaypudyrskaya Bay, with only 0–20 species of macrobenthos observed (Kucheruk et al., 2003; Denisenko et al., 2003; Denisenko, 2013). Kucheruk has reported that the first metres of the near-shore sandy shallows (0–2 m) are not suitable for macrobenthos due to severe wave disturbance, and macrobenthos only appear in the Pechora Sea below the 5–7 m isobath and the highest productivity below pycnocline in the low temperature high salinity Arctic waters (Kucheruk et al., 2003). Relatively low biodiversity (but high biomass) has been also noted for the deepest area of the Pechora Sea, the Prinovozemelskiy Trough (180–210 m). This area is characterised by 10–20 species, a biomass of approximately 100 g/m^2, and dominated by the bivalve mollusc *Macoma calcarea*, brittle star *Ophiocten sericeum* (Forbes, 1852), sipunculid *Golfingia margaritacea* (Sars, 1851) and other species (Antipova, 1973). The rest of the Pechora Sea typically lies within water depth range 20–60 metres and is characterised by a higher number of species (50–60) but fluctuating biomass ranging from <10 to >500 g/m^2 (Denisenko et al., 2003; Denisenko, 2013). Areas of the high biomass of macrobenthos may be linked to the intensity of sedimentation processes and can be related to concentration of the C_{org} in the bottom sediments (Antipova, 1973; Denisenko, 2013).

Researchers distinguish different communities of macrobenthos with the latest classification describing 13 macrobenthic assemblages (Denisenko et al., 2003), but all seem to agree that overall macrobenthos of the Pechora Sea is dominated by bivalve molluscs and most common include *Astarte borealis*, *Astarte montagui*, *Ciliatocardium ciliatum*, *Macoma calcarea*, *Serripes groenlandicus* and others (Brotskaya and Zenkevich, 1939; Antipova, 1973; Pogrebov et al., 1997; Dahle et al., 1998; Denisenko et al., 2003; Kucheruk et al., 2003). In addition, subtidal aggregations of the blue mussel *Mytilus edulis* Linnaeus, 1758 with mean biomass of approximately 1100 g/m^2 have been discovered near Dolgy Island (Sukhotin et al., 2008).

Some authors have previously noted that mobile fauna such as gastropod molluscs (Buccinidae) and decapod crustaceans, and infauna of the hard substrates are underrepresented in grab samples due to the mechanics of sampling and therefore the benthic samples are not fully representative of the real biomass and biodiversity of seafloor invertebrates (Antipova, 1973). Presence of mobile benthic decapods, including the newly introduced invasive snow crab *Chionoecetes opilio* is also highlighted in the GPNS reports 2015–2017 from *Prirazlomnoye* oil field (Gazprom, 2018).

2.2.3. Knowledge gaps

Despite the high number of expeditions carried out in the region, knowledge gaps in understanding of diversity, composition, distribution and dynamics of macrobenthos of the Pechora Sea still exist. This is evident in a number of ways. First, there is a mismatch between the number of study sites in the open-sea versus the near-shore areas (Denisenko N. et al., 2019). Most of the benthic surveys in the Barents Sea were conducted on-board large research vessels, and the upper depth limit of these studies was about 10 m, which is why near-shore shallows are still massively under-reported. More recent attempts to address this have been undertaken at Dolgy Island (Denisenko S. et al., 2019; Sukhotin et al., 2008), however, macrobenthos from most of the shallow-water parts of the Pechora Sea remains poorly studied.

Second, there is a significant lack of time series data. The majority of existing manuscripts focus on outcomes of just one or two years of sampling (e.g. - Dahle et al., 1998; Denisenko et al., 2003; Kucheruk et al., 2003; Sukhotin et al., 2008; Denisenko, 2013; Denisenko S. et al., 2019); some others compare their results with earlier years although sampling often occurred in different locations and with different sampling gear (Antipova, 1973; Pogrebov et al., 1997). Only very limited research has investigated interannual variability of macrobenthos in more detail, example being the latest review of long-term dynamics of macrobenthos published by Stanislav Denisenko in 2013. However, his extensive review assessed available data collected prior to 1995, it therefore lacks data from the later 25 years, which is crucial in the context of ongoing climate change in the

Arctic. Time series data from more recent years are produced by the ecological monitoring programmes by the oil and gas companies, in which the same sites are sampled annually, but most of these data remain confidential.

Lastly, lack of consistency in methods and sampling gear in benthic research in the Pechora Sea means a lack of comparability between studies and needs to be addressed. Historically, different sampling gear were used for benthic studies, including benthic grabs of different models and sample area (0.1 m^2 versus 0.25 m^2), benthic trawls, quadrats, underwater photography, or more lately, remotely operated vehicles (ROV). Differences, advantages and requirements of these techniques have not been addressed in the literature in detail with regards to regional conditions and it is therefore important for further research and monitoring to develop a more integral and standardised approach to assessments of benthic communities, both in terms of number of sampling sites, research areas, indicator species and sampling techniques.

This thesis aimed to address all three major knowledge gaps by (1) improving baseline knowledge on macrobenthos by conducting historic review (Chapter 1) and generating new data on shallow-water macrobenthic communities; (2) assessing interannual variability of macrobenthos in one of the research areas; (3) building knowledge to provide recommendations for systematic ecological monitoring (Chapter 5).

2.2.4. Objectives and scope of this Chapter

This chapter is focused on assessing the current state and interannual variability of macrobenthos in the Pechora Sea. **Aims of this chapter** were to collect new baseline data characterising the state of the shallow-water macrobenthos of the Pechora Sea, and to assess temporal variability in composition and biomass of benthic communities.

More specifically, this chapter had the following **research objectives**:

1) To provide new data on the current state of macrobenthos in the under-reported areas of the Pechora Sea, particularly in the shallow waters of the Pechora Bay.
2) To characterise in detail the state and structure of macrobenthic communities in important foraging grounds of the Atlantic walrus near Vaigach Island.
3) To assess interannual variability of the Pechora Sea macrobenthos by analysing time series data collected from the research area near Vaigach Island in 2015–2020, to identify and characterise potential drivers of change.

To address these objectives, an attempted comprehensive data set was generated, comprising field samples collected by the author during the RV *Kartesh* research expeditions to the Pechora Sea in 2016–2018, with additional data from expeditions in 2015, 2019 and 2020 provided by the Lomonosov Moscow State University Marine Research Center (LMSU MRC). Field sites were chosen based on literature review and knowledge gaps identified.

2.3. Methods

2.3.1. Research areas and sampling

Samples of macrobenthos used in this study were collected from the two research areas in the Pechora Sea – (1) the continental shallows of the Pechora Bay; (2) water territory near Vaigach Island. The first area corresponds to the less studied communities of the shallow waters at the margins of their distribution. Specifically, the shallows of the Nenetsky Nature Reserve have never been previously described in the literature. The second research area lies within the foraging grounds of the Atlantic walrus between Vaigach, Dolgy and Matveev Islands and presumably contains important feeding resources (Semenova et al., 2019; Denisenko S. et al., 2019). Baseline surveys were conducted in both research areas in the summer of 2016. In the second research area, selected sites were sampled continuously thereafter over five years (2015–2020) to assess interannual variability.

Pechora Bay

The first study area was within the Pechora Bay, the large estuarine ecosystem that assures a huge proportion of continental run-off into the Barents Sea region. The Pechora Sea receives approximately 2.5 million tonnes of terrigenous sediments annually through the Pechora estuary (Dobrovolsky and Zalogin, 1982). The Pechora Bay is characterised by broad intertidal zone, with a tide height of 1.1–1.5 m (Byshev et al., 2003; Denisenko N. et al., 2019). The ice thickness in winter reaches 1.5 m, freezing to the bottom of the shallow near-shore areas of the bay. Sediments in the bay are formed by clayey sands and are influenced by continental run-off and permafrost abrasion (Denisenko N. et al., 2019).

The research area lies within the 1st zone of the Nenetsky State Nature Reserve, the "*Pechora River estuary and a 2 km water territory surrounding the Russky Zavorot peninsula*". Macrobenthic assemblages have not been previously studied in the shallows of the continental shore of the reserve.

Benthic samples from the Pechora Bay were collected in one year only, between the 24th and 30th August 2016 in the Nenetsky State Nature Reserve from the inner (southern) bay of the Russky Zavorot Peninsula (Figure 2.3-1). The inner coastline of the Kuznetskaya inlet forms a shore of the Pechora Bay and is comprised of wetlands, protected from the waves, and covered by vegetation.

Bottom sediments were formed of homogeneous sand with silts across the whole sampling area. Samples were taken at 8 sampling sites (Figure 2.3-1) in 3 replicates from each site in the depth range between 1.1 to 1.8 m at low tide from a rubber motorboat with a hand shovel with capture area of 0.05 m^2 (20 x 25 x 20 cm). Sediments were washed over a mesh size of 0.5 mm with sea water then all macrobenthos were pre-fixed with 4% formalin solution until laboratory.

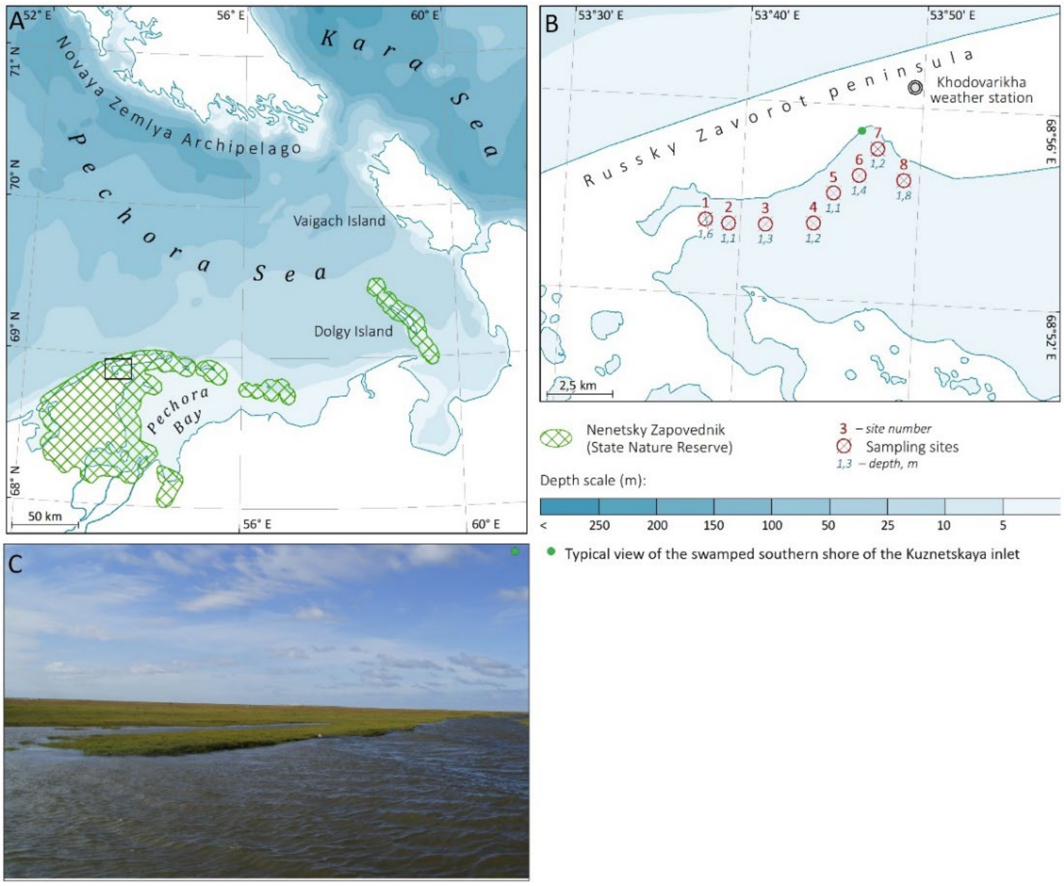


Fig. 2.3 - 1. Map of the study area in the Pechora Bay: (A) Study area (black rectangular) and territory under protection of the Nenetsky Nature Reserve (green hatching); (B) Sampling sites with bathymetry data shown for each site; (C) Typical view of the swamped southern shore of the peninsula open to the Kuznetskaya inlet. Figure published in Gebruk et al., 2019.

Vaigach Island

The recent satellite telemetry study of the walruses’ movements in the Pechora Sea has identified three key areas used by the walruses in the Pechora Sea – (1) summer haul-out site in Vaigach Island; (2) summer haul-out site in Matveev Island; (3) water territory between the islands (Semenova et al., 2019). It has been also hypothesised that the water area between Vaigach and Matveev Islands serves as the key foraging ground for the walruses in summer and this area was chosen as a focus of the present study.

Macrobenthos near Vaigach has not been explicitly studied, with only a couple of sampling sites previously investigated in the area. Overall, the research area is characterised by a high biomass of bivalve molluscs and falls into the transition area between *Spiochaetopterus typicus* M Sars, 1856 – *A. borealis* community and *S. groenlandicus* – communities according to the latest benthic habitat mapping in the Pechora Sea (Denisenko et al., 2003, Figure 2.3-2).

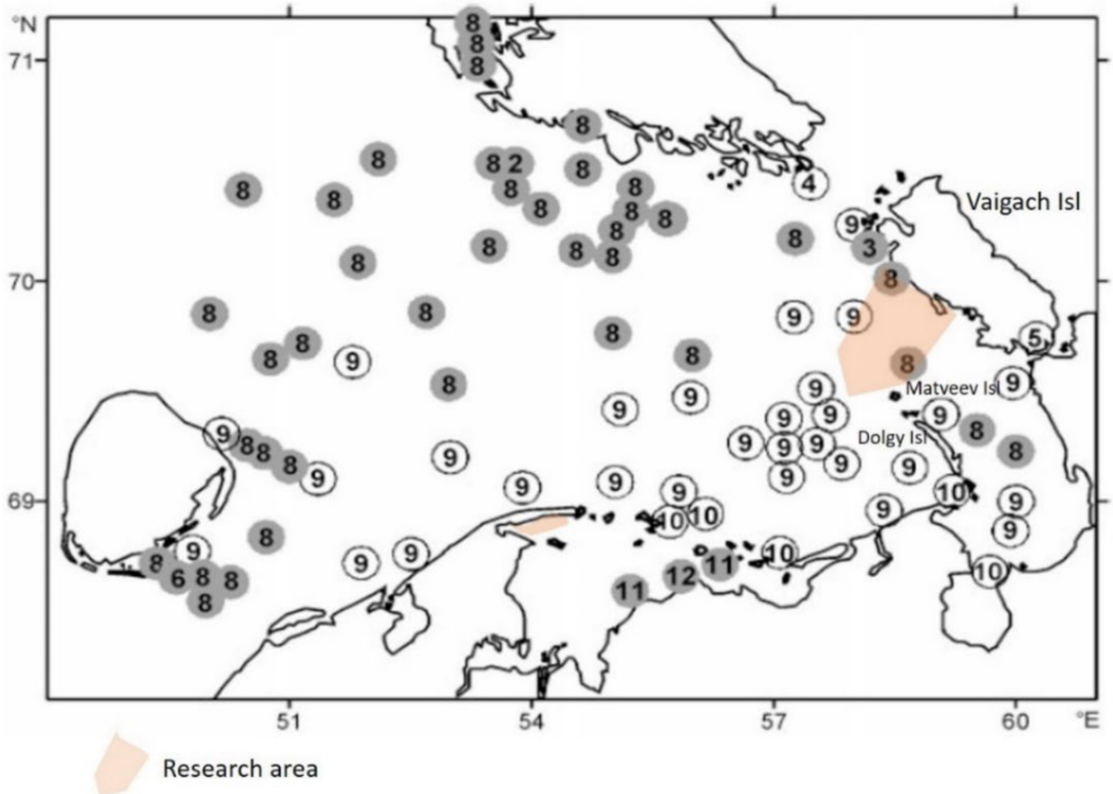


Fig. 2.3 - 2. Macrobenthic communities of the Pechora Sea according to Denisenko et al., 2003. The most abundant benthos were: 8 - *Spiochaetopterus typicus – Astarte borealis*, 9 - *Serripes groenlandicus.* Map adapted from Denisenko et al., 2003.

Benthic surveys in the nearshore waters between Vaigach, Matveev and Dolgy Islands were conducted on-board the RV *Kartesh* in 2015–2020 over an area of ~2425km^2. Of the six years of sampling, the most detailed survey was conducted in 2016, comprising 19 sites in the depth range from 9 to 66 metres; in the other years, the number of sites varied from 2 to 14 (Figure 2.3-4). Samples were collected during the expeditions in 2016–2018 by the author, additional samples from 2015, 2019 and 2020 surveys were provided for this study by the LMSU MRC as outlined in more detailed in the Research approach and data integration Chapter. Benthic grab samples were taken each year using the *Okean-50* bottom grab with sampling area of 0.175 m^2, or the *Okean-0.1* grab with sampling area of 0.1 m^2. Bottom sediments from the grab were washed over a 0.5 mm mesh with seawater (Figure 2.3-3). All macrobenthos were then fixed with 4% formalin solution and stored in labelled buckets.

Fig. 2.3 - 3. Deployment of the benthic grab Okean-50 during the RV *Kartesh* expedition in 2018 (on the left); washing of the sediments from the grab over the upper mesh (5 mm) of the washing table in 2016 (on the right). Photo courtesy of the LMSU MRC.

2.3.2. Processing of the samples

In the laboratory, all specimens of macrobenthos were washed in freshwater, sorted and re-fixed in 70% ethanol. Macrobenthic invertebrates were studied under stereo microscopes and identified using morphological features to species level where possible, to genera or family in the other cases, Nemerteans and Nematodes - to phylum. The following identification keys were used: Gaevskaya, 1948; Guryanova, 1951; Dyakonov, 1954; Zhirkov, 2001; Naumov, 2006. All taxon names were standardised in accordance with the World Register of Marine Species (WoRMS, 2021).

For each sample, taxa were counted, air dried on filter paper until no drops of excess ethanol drops were visible, and then weighed on the Jewelry Scale (ML-CF3 – reported wet mass accuracy 0.001 g). Unidentified fragments were also weighed, recorded and marked as “Rest”. Polychaeta with secretory tubes were taken out before counting except *Galathowenia oculate* (Zachs, 1923): these were weighed in tubes to prevent destroying the individuals. Bivalve molluscs and gastropods were weighed in their shells. Animals that were presumably dead before sampling (decayed organic matter) were not studied as well as empty shells. Individual specimens of Hydrozoa and Bryozoa colonies were not counted but noted in protocols as colonies.

Samples collected in 2016 were identified by the author and Maria Mardashova, samples collected in other years were identified by the taxonomy specialists from IO RAS (Miloslav Simakov, Alexander Basin) and LMSU MRC (Maria Mardashova, Maria Fedyaeva, Sergey Gorin).

2.3.3. Data analysis

Mean values ± standard deviations were measured for biomass (g/m^2) and abundance (ind./m^2) to characterise macrobenthos. In addition, "relative production" parameter was calculated as a relationship between biomass and abundance based on average exponent of annual relative production on body-size for macrobenthic invertebrates following Clarke and Warwick (2001):

$$P=(B/A)^{0.73} \times A$$

Where *B* refers to biomass, *A* refers to abundance, 0.73 refers to average exponent of annual relative production on body-size for macrobenthic invertebrates.

Statistical calculations were performed using free software PAST version 3.22 (Hammer and Harper, 2006), unless otherwise specified. To characterise diversity of macrobenthos standard diversity indices including dominance, Simpson index and Shannon index were used based on abundance data (Hammer and Harper, 2006). To assess predicted species richness ($\tilde{S}$) in the research area, a species accumulation curve (sample rarefaction curve) was calculated using the Chao-2 type estimator as the following:

$$\tilde{S} = S_{obs} + \frac{(H-1)s_1^2}{2Hs_1}$$

Where *H* refers to samples, S_{obs} refers to the total number of observed species and S_1 refers to the number of species found in exactly one sample.

Types of macrobenthic communities were defined by biomass data. The species with the highest biomass at sampling sites were considered dominants; second, third and fourth highest – as subdominants. The non-metric multidimensional scaling (nMDS) based on the Bray-Curtis similarity index and the hierarchical cluster analysis based on an unweighted pair group method with arithmetic mean (UPGMA) algorithm with Bray-Curtis similarity index were used to distinguish underlying structure to macrobenthic communities.

To assess significance of differences between the macrobenthic communities identified by nMDS/UPGMA clusters, or between macrobenthic communities in different years of sampling, a one-way pairwise analysis of similarities (ANOSIM) analysis was performed on matrixes of relative fractions of each species biomass to mean biomass per sample (g/m^2) and relative fraction of each species abundance to mean abundance per sample (ind./m^2). P-values of each pair were given, with sequential Bonferroni corrections applied. Contribution of species to observed differences was assessed using similarity percentage (SIMPER) analysis based on Bray-Curtis similarity measure. One-sample Wilcoxon signed-rank test for given median M (nonparametric) was used to compare mean biomass and mean abundance values between the years.

To assess contribution of different parameters (sampling gear, year of sampling, sampling site) to the observed variation the PERMANOVA (Non-Parametric Permutational Multivariate Analysis of Variance) (permutation N=999) was performed (Euclidean distance) in PRIMER statistical package (Anderson et al., 2015).

A constrained seriation algorithm (Hammer and Harper, 2006), based on the presence-absence matrix for all years, was used to order the species according to when they appeared or disappeared in the samples. Only species that were found in more than one sample were considered for inclusion in such ordering. Biogeographical classification of species was given following CAFF (2013) and Mironov (2013) and included the following categories: a – Arctic; b-a – boreal-Arctic, w – widespread (subtropics to Arctic). Information on distribution ranges of species was obtained from Ocean Biodiversity Information System database (OBIS, 2021), WoRMS, and primary literature (e.g., for polychaetes – Zhirkov (2001); for bivalves – Naumov (2006); for amphipods – Guryanova (1951), for other Pechora Sea macrobenthos – Denisenko (2013)).

Maps were generated using ArcMap v10.4.1. using the standard geoprocessing tools with the reference coordinate system UTM/WGS84 Zone 40N with technical assistance of the LMSU MRC cartographer, Yulia Ermilova.

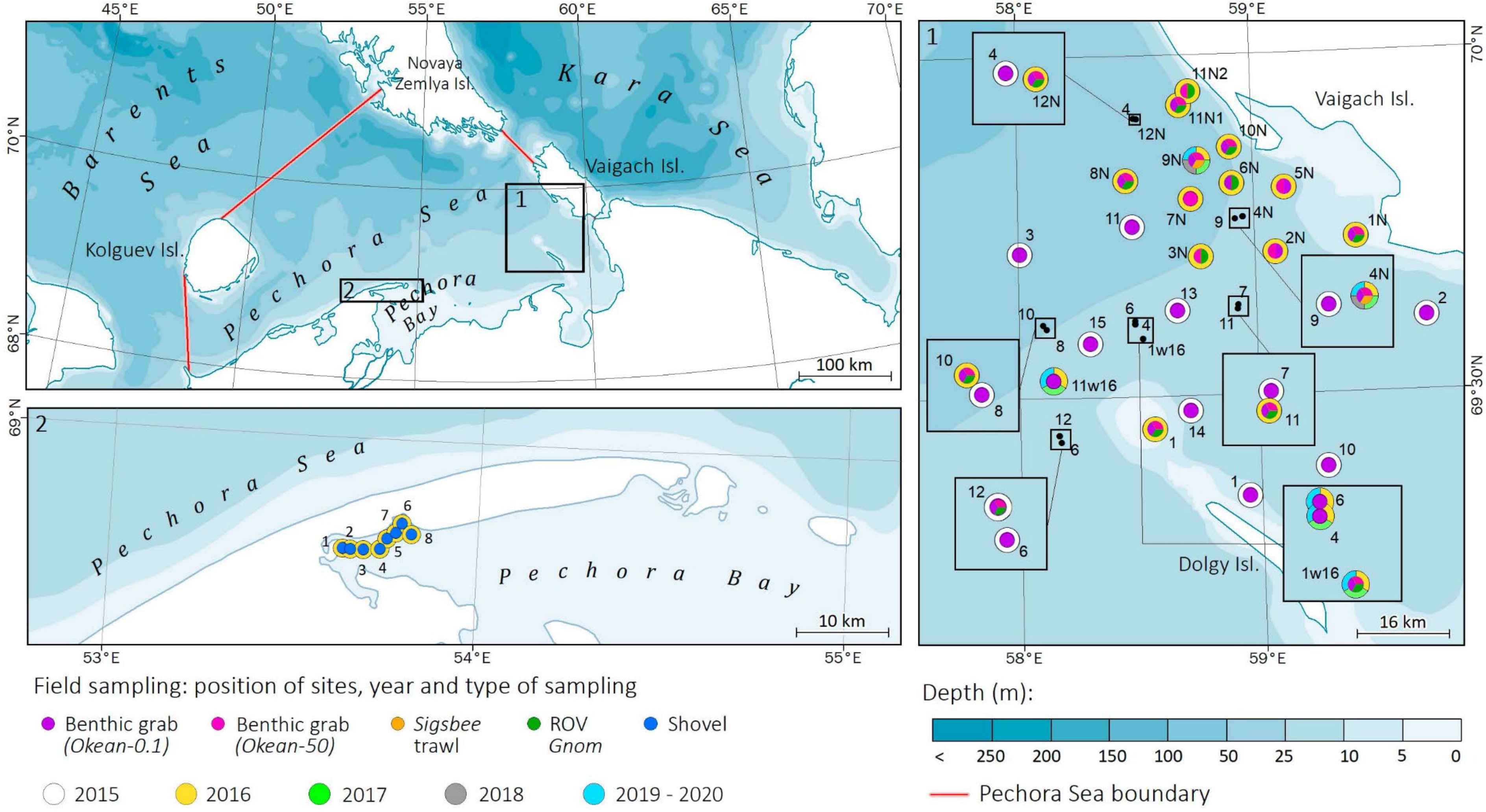


Fig. 2.3 - 4. Position of sampling sites in 2015-2020 in the Pechora Sea. Sampling gear and sampling years are shown for each year by different colours. Map courtesy of the LMSU MRC.

2.4. Results

2.4.1. Macrobenthos of the Pechora Bay in 2016 (published in Gebruk et al., 2019)

A total of 14 taxa of benthic invertebrates were identified in 24 samples from 8 sampling sites in the Pechora Bay in 2016, 12 taxa identified to species or morphospecies level (Table 2.4-1). Fauna mainly comprised of crustaceans (5 species), polychaetes (4 species) and bivalves (3 species), with single a species of Priapulida and Insecta. Bivalves were the dominant group by both the total biomass and abundance. The mean biomass of macrobenthic invertebrates in the area was 21.31±0.32 g/m^2 and the mean abundance 2131±1825 individuals per m^2 (ind./m^2).

Table. 2.4 - 1. Species composition of macrozoobenthos and mean values of biomass (g/m^2) and abundance (ind./m^2) of each species in the study area in 2016. Table published in Gebruk et al., 2019.

Class	**Species**	**Mean biomass, g/m^2 (±St.Dev)**	**Mean abundance, ind./m^2 (±St.Dev)**	**Habitats***
Bivalvia	*Cyrtodaria kurriana* Dunker, 1861	0.18±0.01	10.83±0.21	m, b
Bivalvia	*Limecola balthica*	17.29±0.19	762.50±7.54	m, b
Bivalvia	*Yoldia hyperborea*	2.87±0.09	595.00±8.05	m
Malacostraca	*Saduria entomon* (Linnaeus, 1758)	0.05±0.001	2.50±0.07	m, b
Malacostraca	*Monoporeia affinis* (Lindström, 1855)	0.006±0.001	2.50±0.07	b, f
Malacostraca	*Pontoporeia femorata* Krøyer, 1842	0.001±0.001	0.83±0.04	m, b
Malacostraca	*Monoculodes* sp.	0.003±0.001	4.16±0.13	m
Malacostraca	*Diastylis sulcata* Calman, 1912	0.005±0.001	6.66±0.13	m, b
Insecta	Chironomidae gen.sp.	0.002±0.003	1.66±0.06	m
Polychaeta	*Eteone* agg. *flava* (Fabricius, 1780)	0.09±0.001	31.66±0.32	m
Polychaeta	*Laonice cirrata* (M. Sars, 1851)	0.001±0.001	0.83±0.04	m, b
Polychaeta	*Micronephthys minuta* (Théel, 1879)	0.009±0.007	6.66±0.09	m
Polychaeta	*Spio armata* (Thulin, 1957)	0.57±0.007	686.66±7.39	m
Halicryptomorpha	*Halicryptus spinulosus* von Siebold, 1849	0.17±0.001	1.66±0.06	m

Note: *Typical habitats are presented according to WoRMS with corrections (Zhirkov, 2001): m – marine, b – brackish, f – freshwater.

Shannon diversity was low (H'=1.26), macrozoobenthos were represented by a small number of taxa with few individuals and strong dominance of few species (Table 2.4-2). The predicted number of species was the same as discovered (Chao-2 richness =14.19). Biodiversity was represented close to equally between the sampling sites: four species had 100% occurrence in the study area, and only one species had <20% occurrence (Table 2.4-2).

Table. 2.4 - 2. Key characteristics of macrozoobenthic diversity in the study area: number of taxa, number of individuals, dominance, Simpson diversity, Shannon diversity, estimated species richness (Chao-2 metric). Table published in Gebruk et al., 2019.

Diversity indices	Values of diversity indices
Taxa_S	14
Individuals	2537
Dominance_D	0.33
Simpson_1-D	0.68
Shannon_H	1.26
Chao-2	14.19

Species accumulation curve approached plateau at the level of 7 sampling sites, reaching 14 species (Figure 2.4-1). The observed diversity of macrozoobenthos was therefore representative for the expected diversity in the area.

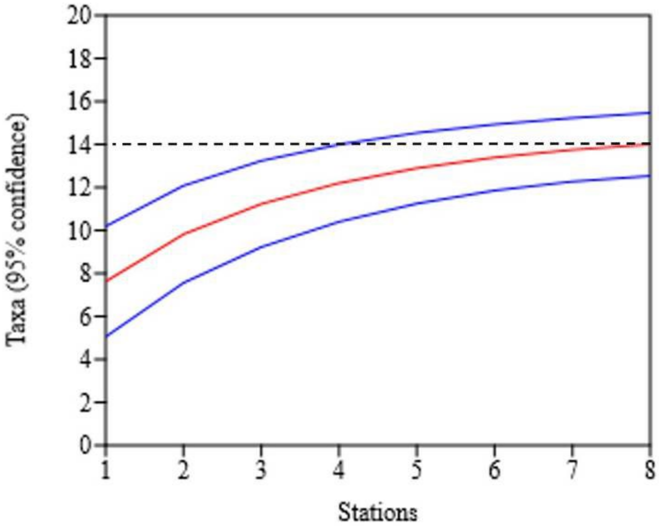


Fig. 2.4 - 1. Sample rarefaction (Mao's tau): red line – accumulated number of species, blue line – 95% confidential interval, black dotted line – number of species found in the samples. Figure published in Gebruk et al., 2019.

The UPGMA hierarchical clustering and nMDS plots showed three groups of sampling sites in the study area (Figure 2.4-2). Group A consisted of sampling sites 5, 7 and 8; group B included sampling sites 2, 3 and 6; and sampling site 1 formed a separate group. ANOSIM analysis showed statistically significant difference between groups A and B (p=0.0283; R=1).

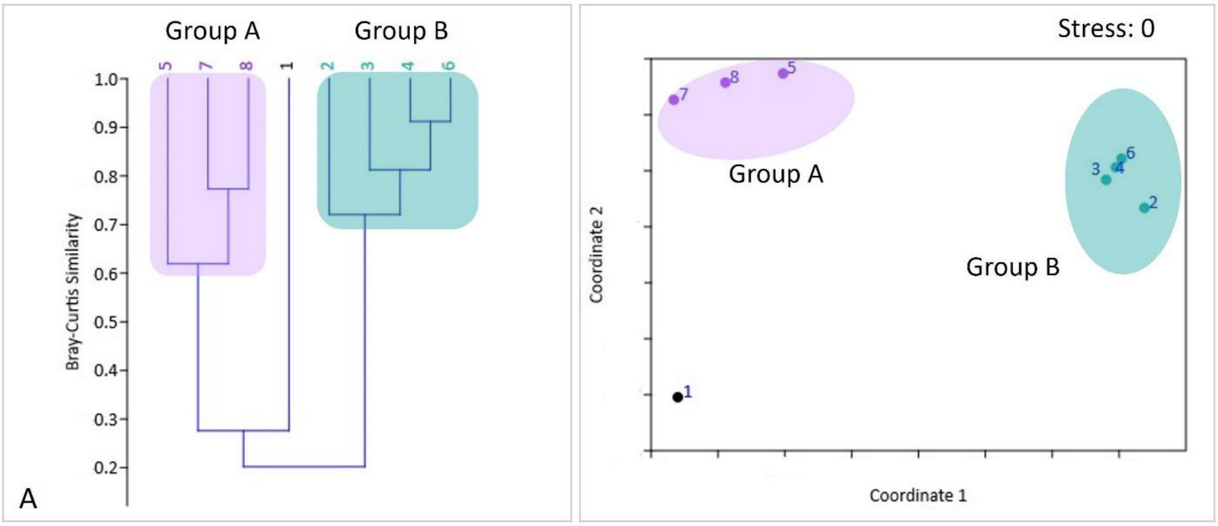


Fig. 2.4 - 2. Groups of sampling sites in the study area determined by the UPGMA hierarchical clustering (carried out on macrozoobenthic biomass data) (A) and MDS (B). Three groups can be seen: (A) Sampling sites 5, 7 and 8, (purple shading); (B) Sampling sites 2, 3, 4 and 6 (green shading); (C) Sampling site 1. Figure adapted from Gebruk et al., 2019.

Variation in biomass of three species (*L. balthica*, *Y. hyperborea* and *S. armata*) drove the difference between the sampling sites as shown by SIMPER analysis (Table 2.4-3). Biomass of the bivalve *L. balthica* accounted for 83.7% contribution to dissimilarity between the groups. Despite the statistical difference between the groups of sampling sites, *L. balthica* remained the dominant species for all the sampling sites in the study area. Macrozoobenthos in the study area was therefore formed by a monodominant community of *L. balthica*.

Table. 2.4 - 3. Species contribution to dissimilarity between groups of sampling sites produced by SIMPER analysis (only taxa with >1% contribution shown). Table published in Gebruk et al., 2019.

Species	Average dissimilarity	Contribution %	Cumulative %	Group A	Group B
Limecola balthica	78.56	83.7	83.7	0.091	4.65
Yoldia hyperborea	11.38	12.13	95.83	0.073	0.793
Spio armata	1.902	2.027	97.85	0.005	0.113

Species composition of each sampling site and spatial distribution of macrozoobenthos biomass (g/m^2) across the study area are shown in Figure 2.4-3. Biomass of macrozoobenthos per sampling site had no correlation with depths range (R=-0.45, p=0.2).

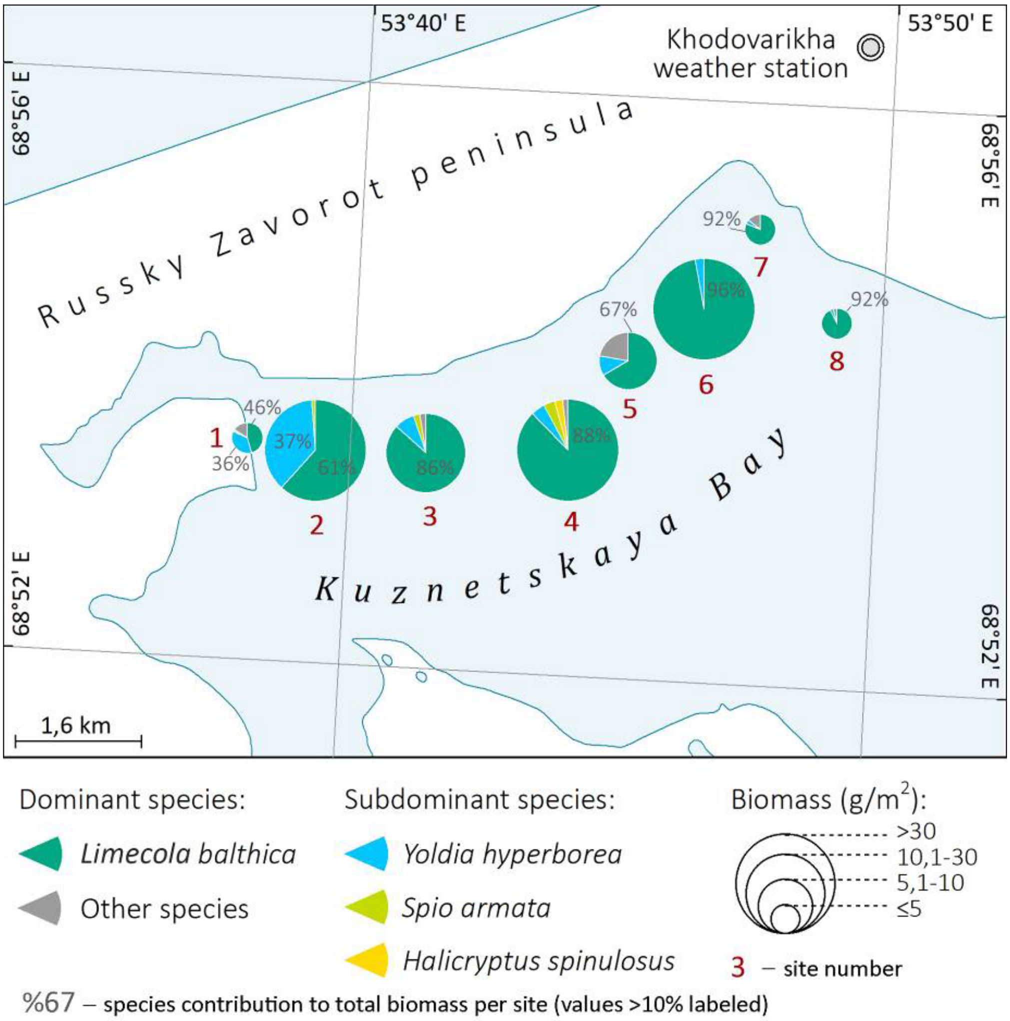


Fig. 2.4 - 3. Macrobenthic biomass by species in Pechora Bay in 2016. Overall biomass and contribution of different species to biomass demonstrated in pie charts for each sampling site. Figure published in Gebruk et al., 2019.

2.4.2. Macrobenthos near Vaigach Island in 2016 (published in Gebruk et al., 2021)

A total of 184 taxa of macrobenthic invertebrates were found near Vaigach Island in 2016, of which 148 were identified to the species level. The richest groups were polychaetes (94 taxa, 76 species); molluscs (36 taxa, 34 species) and crustaceans (34 taxa, 25 species). Other taxonomic groups, including brachiopods, bryozoans, cnidarians, echinoderms, foraminifers, nemertean, priapulids, pycnogonids and sipunculid worms were represented in minor proportions. Mean species richness was 21.57±8.68, ranging from 8 to 41 taxa per sampling site. The total number of species predicted for the area by Chao-2 estimator was 204±28, the species accumulation curve was approaching the saturation level but did not reach it (Figure 2.4-4). High values of the Simpson diversity index (0.8±0.1) indicated heterogeneous communities with low dominance of single taxa (D=0.19±0.1). Communities overall exhibited a relatively high Shannon entropy index (2.26), i.e., communities contain many taxa, but each represented by only a few individuals (Hammer and Harper, 2006).

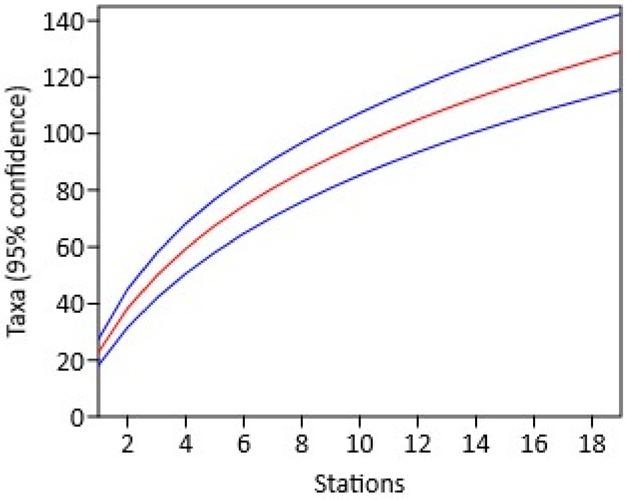


Fig. 2.4 - 4. Sample rarefaction curve: red line – accumulated number of species, blue lines – 95% confidential interval. Figure published in Gebruk et al., 2021.

Mean abundance was 370±14 ind./m^2 ranging from 86±3 ind./m^2 (sampling site 1) to 869 ind./m^2 (sampling site 10). Mean biomass was 222.06±229.02 g/m^2 ranging from 10.57±0.41 g/m^2 (sampling site 7N) to 693.47±39.87 g/m^2 (sampling site 9N). The bivalve molluscs *Astarte borealis, Ciliatocardium ciliatum* and *Astarte montagui* together comprised 66% of the total biomass, accounting for 30%, 21% and 15% respectively. All other taxa contributed less than 10% each to the total biomass, with 118 taxa contributing less than 1% each.

The UPGMA clustering and nMDS revealed three groups of sampling sites in the study area: (1) – *A. borealis*-community; (2) *A. montagui* - *Macoma calcarea* – community; (3) *C. ciliatum* – community (Figure 2.4-5). Group 1 was strongly dominated by *A. borealis* (sampling sites 8N, 9N, 10N and 1w16 in the north-west and central areas); it had the highest mean biomass (289.73±14.94 g/m^2) and a total of 65 taxa –the maximum among the sampling sites (ranging from 18 to 41 per sampling site). Sampling sites within group 2 (sampling sites 10, 12N, 11N2, 7N, 3N, 11N1, 4N) were dominated by *A. montagui* and *M. calcarea* with various subdominants, including *Y. hyperborea*, *Nephtys ciliata* (Müller, 1788) and *G. margaritacea*. Group 2 was characterized by low mean biomass (41.05±1.5 g/m^2) and high species richness (n=74; 14 – 34 per sampling site). Group 3 (sampling sites 6, 11w16, 4, 11, 1N) was mainly concentrated in the shallow waters in the south-east area close to Matveev Island. The biomass was formed by large bivalves, *C. ciliatum* and *S. groenlandicus*, with contributions from *A. montagui* and *Ophelia limacine* (Rathke, 1843). Group 3 was characterized by high biomass (248.5±12.95 g/m^2) and relatively low richness (n=60; 15–30 species per sampling site). The remaining three sampling sites (sampling sites 1, 2N, 5N) had the lowest biomass (35.48±1.5 g/m^2) and richness (n=47; ranging from 9 to 27 per sampling site). Dominants in terms of biomass were *Pectinaria hyperborea*, *Hamingia arctica* Danielssen & Koren, 1880 and *Y. hyperborea* for sampling sites 1, 2N and 5N, respectively.

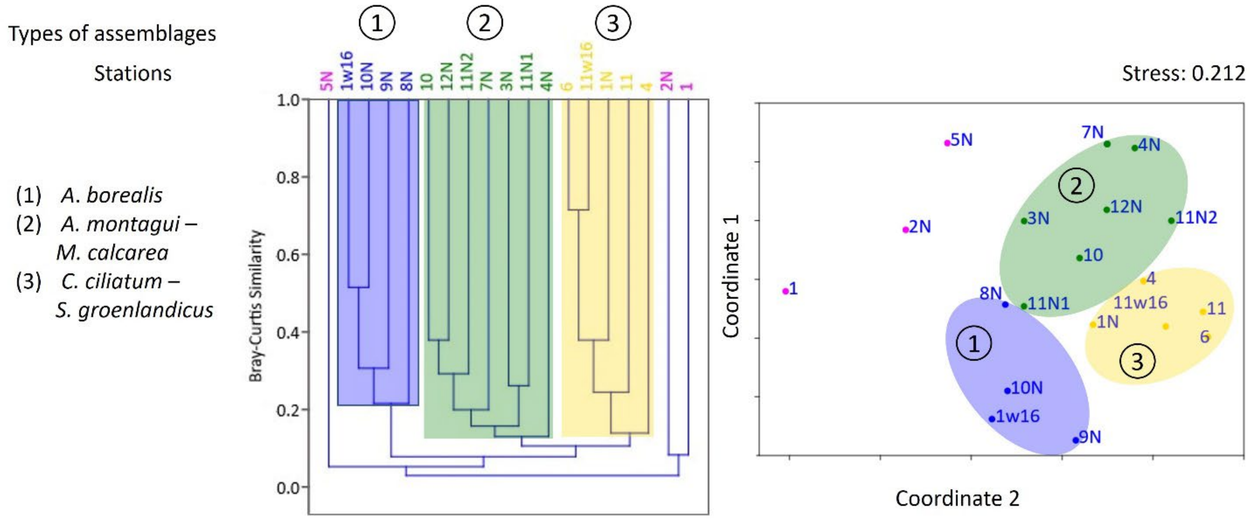


Fig. 2.4 - 5. Groups of sampling sites based on UPGMA hierarchical cluster analysis (on the left) and nMDS (on the right), both calculated with Bray-Curtis similarity measure. Groups of sampling sites were the following: (1) 1w16, 10N, 9N, 8N – *Astarte borealis*-community; (2) 10, 12N, 11N2, 7N, 3N, 11N1, 4N – *A. montagui-M. calcarea* - community; (3) 6, 11w16, 4, 11, 1N – *C. ciliatum-S. groenlandicus* - community.

According to the ANOSIM test groups 1 and 2 and groups 2 and 3 were statistically significantly different ($p<0.05$, Table 2.4-4), but not the others.

Table. 2.4 - 4. Pairwise comparison of groups of sampling sites with ANOSIM analysis, p-values with sequential Bonferroni significance showed with green shading. Table published in Gebruk et al., 2021.

	1	2	3
2	p=0.01; R=0.62		
3	p=0.09; R=0.19	p=0.01; R=0.65	
4	p=0.48; R=0	p=0.81; R=-0.29	p=0.764; R=-0.2

Total biomass (g/m^2) and proportions of dominant and subdominant species for each sampling site are shown in Figure 2.4-6.

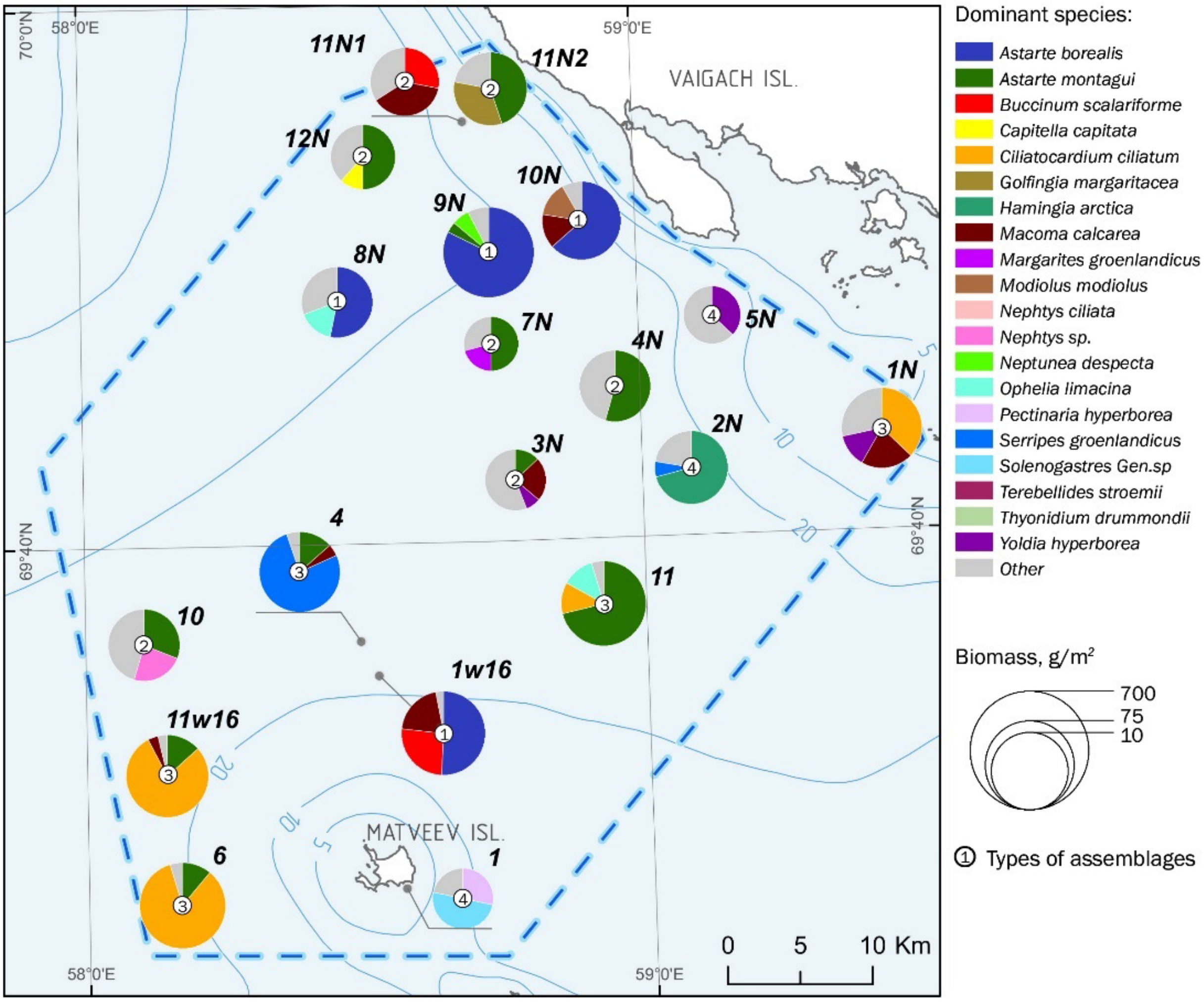


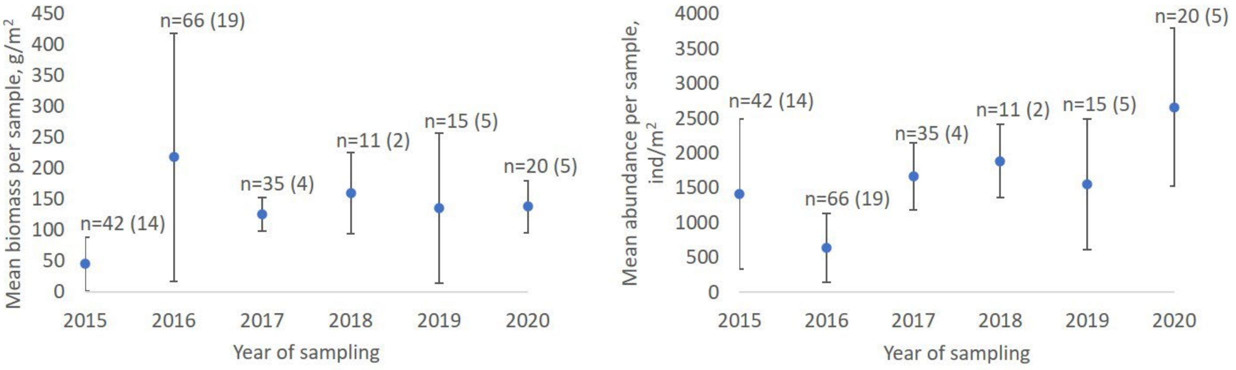
Fig. 2.4 - 6. Macrobenthic diversity in the research area: species composition and biomass for each sampling site are shown in the pie charts proportional to total biomass per sampling site (dominant and subdominant in biomass species shown by different colours, with the list of species in the legend). Number in the centre of pie chart shows the type of macrobenthic assemblage. Figure published in Gebruk et al., 2021.

Macrobenthos in the research area was highly heterogeneous. The biomass and species composition per sampling site varied greatly: species dominating the biomass were different at 62% of the sampling sites. The overall macrobenthos biomass in the area, however, was dominated by three species of bivalve molluscs: *A. borealis* (30% of the total biomass), *C. ciliatum* (21%) and *A. montagui* (15%). In general, macrobenthos in the research area comprised highly heterogeneous community of bivalves, *A. borealis* – *C. ciliatum*.

2.4.3. Interannual variability of macrobenthos in the Pechora Sea

Biomass and abundance

During the six years of sampling (2015–2020) a total of 345 taxa of macrobenthic invertebrates were observed with varying species richness each year, ranging from 106 species in 2018 to 184 species in 2016. Polychaetes remained the most species-rich group for all years, whereas bivalve molluscs dominated overall biomass in all sample years. Mean biomass of all macrobenthos per sampling site was lowest in 2015 (44.63±43.31, g/m^2) and highest in 2016 (217.48±200.49, g/m^2) with no clear trend observed through the years (Figure 2.4-7), and no statistically significant differences between the medians (Wilcoxon p=0.9). Mean abundance of macrobenthos per sampling site was highest in 2020 (2658±1137, ind./m^2) and lowest in 2016 (638±492, ind./m^2) and no clear trends or statistically significant differences (Wilcoxon p=0.8) were observed for mean abundance of macrobenthos in different years either (Figure 2.4-7).



n – number of samples (number of sampling sites in brackets)

Fig. 2.4 - 7. Mean biomass of macrobenthos per sample ± St.Dev (g/m^2) (on the left) and mean abundance of macrobenthos per sample ± St.Dev (ind./m^2) (on the right) for each year of sampling. Number of repeats (samples) and number of sampling site (in brackets) shown for each value.

Composition of macrobenthos

The variation in composition of macrobenthos between the years was assessed. Matrixes of relative fractions of each species biomass to mean biomass per sample (g/m^2) and relative fraction of each species abundance to mean abundance per sample (ind./m^2) were created. Pairwise comparison of the biomass data between the years with ANOSIM revealed significant differences (sequential Bonferroni significance) in composition of macrobenthos between 2015 and 2017; 2015 and 2019 and between 2015 and 2020, all other pairs did not show statistically significant difference (Table 2.4-5). For the abundance data only one pair showed statistically significant differences (sequential Bonferroni significance) – 2015 and 2019 (Table 2.4-6).

Table. 2.4 - 5. Pairwise comparison of the **biomass** data between the years with ANOSIM analysis (sequential Bonferroni significance p'<0.05 shown with green shading).

	2015	2016	2017	2018	2019
2016	p=0.14; R=0.15				
2017	p=0.01; R=0.44	p=1.00; R=-0.17			
2018	p=0.12; R=0.82	p=1.00; R=0.08	p=1.00; R=0.71		
2019	p=0.01; R=0.77	p=1.00; R=0.19	p=1.00; R=0.03	p=1.00; R=-0.16	
2020	p=0.01; R=0.66	p=1.00; R=0.04	p=1.00; R=0.02	p=1.00; R=0.16	p=1.00; R=0.05

Table. 2.4 - 6. Pairwise comparison of the **abundance** data between the years with ANOSIM analysis (sequential Bonferroni significance p'<0.05 – all p-values are not significant).

	2015	2016	2017	2018	2019
2016	p=1.00; R=0.02				
2017	p=1.00; R=-0.20	p=1.00; R=-0.23			
2018	p=0.36; R=0.58	p=1.00; R=0.25	p=0.98; R=1.00		
2019	p=0.01; R=0.69	p=0.09; R=0.45	p=0.11; R=073.	p=0.77; R=0.94	
2020	p=1.00; R=0.23	p=1.00; R=0.04	p=0.47; R=0.41	p=0.73; R=0.74	p=0.1; R=0.79

To assess which species contributed to observed differences, SIMPER analysis was used. Table 2.4-7 demonstrates the outcomes for the pairs of years identified by ANOSIM analysis above, species that contributed to >10% of overall dissimilarity are shown. Observed differences in biomass were predominantly driven by contributions from three species of bivalve molluscs – *S. groenlandicus*, *A. montagui* and *A. borealis*. Notably the biggest contribution to observed differences in biomass was made by different species in different years - *S. groenlandicus* contributed most (14%) to differences between 2015 and 2017; *A. montagui* contributed 12% to differences between 2015 and 2019; and *A. borealis* contributed 17% to differences between 2015 and 2020. Another 15 species contributed between 1 and 8% in different years. Two polychaete species - *Flabelligera affinis* M. Sars, 1829 and *G. oculata* contributed most to observed differences in abundances between 2015 and 2019 (Table 2.4-7), with additional contributions of 1–5% from 19 other species.

Pooling all years together, biomass data showed overall 86.6% dissimilarity between the years with only two species contributing >10% to dissimilarity – bivalve molluscs *A. borealis* (18.2%) and *S. groenlandicus* (10.36%) and 13 species contributing >1% to overall dissimilarity (list of species with cumulative contributions and mean values per each year provided in Appendix 2-1). Abundance data revealed 75.6% overall dissimilarity to which polychaete species *G. oculata* contributed 11.18% and another 15 species contributed >1% (Appendix 2-1).

Table. 2.4 - 7. Outcomes of SIMPER analysis: species contributions to observed differences in biomass and abundance between the years

Species	**Average dissimilarity**	**Contribution to dissimilarity %**
2015 – 2017 (Biomass). Overall average dissimilarity: 84.83		
Serripes groenlandicus	14.04	16.55
Astarte montagui	11.27	13.29
Astarte borealis	11.26	13.27
2015 – 2019 (Biomass). Overall average dissimilarity: 93.58		
Astarte montagui	11.51	12.3
Astarte borealis	9.796	10.47
2015 – 2020 (Biomass). Overall average dissimilarity: 89.65		
Astarte borealis	17.48	19.49
Serripes groenlandicus	12.57	14.02
Astarte montagui	11.51	12.84
2015 – 2019 (Abundance). Overall average dissimilarity: 76.98		
Flabelligera affinis	11.04	14.35
Galathowenia oculata	8.762	11.38

Variance of sampling parameters

To estimate the amount of variation of macrobenthos attributed to different parameters of sampling, the PERMANOVA algorithm was used, and three variables (factors) were considered in the model – (1) year of sampling; (2) sampling site (location); (3) sampling gear.

At the first run of the model, sampling gear showed a negative value of estimate of component of variation and was therefore excluded from the further analysis. After the second run of the model the year of sampling was ranked slightly higher than the sampling site location (Estimate component of variation (Year) =5613; Estimate component of variation (Sampling site) =7257), and interaction of these two components was considered statistically meaningful (p=0.001; Pseudo-F=4.86; dF=10) and most important component of variation (Estimate component of variation (Year X Sampling site) =18006). Full outcomes of PERMANOVA are provided in Appendix 2-2.

Sampling site trajectories

Non-metric MDS plots based on Bray-Curtis similarity index were calculated for each individual sampling site that was repeatedly sampled for over two years based on the relative fractions of relative production of species to mean relative production (Figure 2.4-8). In addition, nMDS plots were created for pooled biomass and abundance data (all sites, repeating sites only, bivalves only, polychaetes only) (Appendix 2-3) and for individual sites based on biomass and abundance data (Appendix 2-4). Results of nMDS ordination for pooled data (Appendix 2-3) did not reveal temporal clustering - all samples fall within the 95% confidence ellipses corresponding to years of sampling, but all ellipses occupy overlapping areas of the graph. Plots of individual sites (Figure 2.4-8) showed that fluctuations of relative production, biomass and abundance had a stochastic character without any pronounced temporal patterns. Raw abundance and biomass data are available, open access with the links provided in Appendix 2-6.

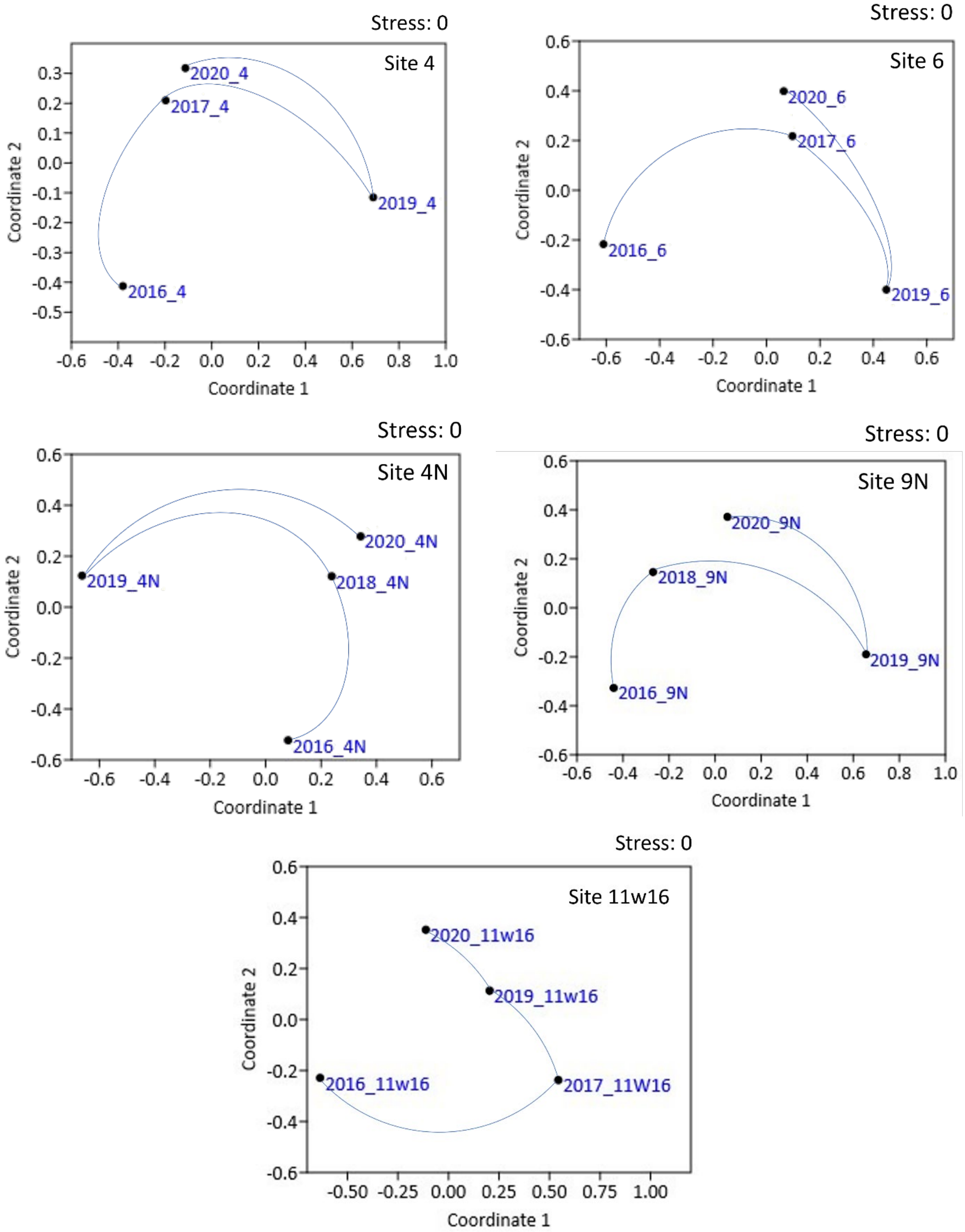


Fig. 2.4 - 8. nMDS plots of relative production (relative fractions of each species relative production to mean relative production per sample for sites that have been sampled over two years, namely – 4, 6, 11W16, 4N and 9N.

Seriation analysis

Finally, to assess dynamics of species composition between the yeas, constrained seriation algorithm was used for presence-absence matrix. Seriation allowed to sort species in a way that showed which species appeared in the research area and which species disappeared. To standardise observations only species that occurred in more than one sample were considered.

Outcomes of the seriation analyses are shown in Table 2.4-8, where presence or absence of appearing and disappearing species in each year is shown as well as their biogeographical classification (following CAFF, 2013; Mironov, 2013). Raw presence/absence data for all years of sampling are presented in Appendix 2-5.

Table. 2.4 - 8. Outcomes of the seriation analysis based on presence/absence matrix.

Group	**Species**	**1**	**2**	**3**	**4**	**5**	**6***	**Biogeography**
		Presence / Absence						**
Polychaeta	*Hamingia arctica*	1	1	0	0	0	0	b-a
Echinodermata	*Stegophiura nodosa* (Lütken, 1855)	1	1	0	0	0	0	b-a
Gastropoda	*Propebela harpularia* (Couthouy, 1838)	1	1	0	0	0	0	b-a
Gastropoda	*Buccinum scalariforme* Kiener, 1834	1	1	0	0	0	0	b-a
Crustacea	*Campylaspis* sp.	1	1	0	0	0	0	w
Polychaeta	*Nicomache minor* Arwidsson, 1906	1	1	0	0	0	0	b-a
Bivalvia	*Astarte elliptica* (T. Brown, 1827)	1	1	0	0	0	0	w
Gastropoda	*Euspira pallida* (Broderip & G. B. Sowerby I, 1829)	1	1	0	0	0	0	b-a
Crustacea	*Leucon pallidus* G.O. Sars, 1865	1	1	0	0	0	0	a
Gastropoda	*Neptunea despecta* (Linnaeus, 1758)	1	1	0	0	0	0	b-a
Polychaeta	*Owenia fusiformis* Delle Chiaje, 1844	1	1	0	0	0	0	w
Crustacea	*Haploops tubicola* Liljeborg, 1856	1	1	1	0	0	0	b-a
Bivalvia	*Pandora glacialis* Leach in Ross, 1819	1	1	1	0	0	0	b-a
Crustacea	*Diastylis rathkei* (Krøyer, 1841)	1	1	1	0	0	0	b-a
Gastropoda	*Margarites helicinus* (Phipps, 1774)	1	1	1	0	0	0	w
Bivalvia	*Astarte montagui*	1	1	1	0	0	0	b-a
Polychaeta	*Heteromastus filiformis* (Claparède, 1864)	1	1	1	0	0	0	w
Polychaeta	*Clymenura polaris* (Théel, 1879)	1	1	1	0	0	0	a
Polychaeta	*Diplocirrus longisetosus* (Marenzeller, 1890)	1	1	1	0	0	0	b-a
Polychaeta	*Aphelochaeta marioni* (Saint-Joseph, 1894)	1	1	1	0	0	0	w
Bivalvia	*Nuculana minuta* (O. F. Müller, 1776)	1	1	1	0	0	0	b-a
Crustacea	*Monoculodes* sp.	1	1	1	1	0	0	w
Sipunculida	*Golfingia margaritacea*	1	1	1	1	0	0	w
Crustacea	*Ampelisca macrocephala* Liljeborg, 1852	1	1	1	1	0	0	b-a
Crustacea	*Pontoporeia femorata* Krøyer, 1842	1	1	1	1	0	0	b-a
Gastropoda	*Margarites groenlandicus* (Gmelin, 1791)	1	1	1	1	1	0	b-a
Polychaeta	*Apistobranchus tullbergi* (Théel, 1879)	0	1	1	1	1	1	b-a
Bivalvia	*Astarte crenata* (Gray, 1824)	0	0	1	1	1	1	b-a
Crustacea	*Protomedeia grandimana* Brüggen, 1906	0	0	0	1	1	1	b-a
Crustacea	*Balanus balanus* (Linnaeus, 1758)	0	0	0	0	1	1	b-a
Crustacea	*Dyopedos bispinis* (Gurjanova, 1930)	0	0	0	0	1	1	b-a
Crustacea	*Leucon nasica* (Krøyer, 1841)	0	0	0	0	1	1	w
Polychaeta	*Ampharete falcata* Eliason, 1955	0	0	0	0	1	1	b-a
Crustacea	*Aceroides latipes* (G.O. Sars, 1883)	0	0	0	0	1	1	a

*1 – 2015; 2 – 2016; 3 – 2017; 4 – 2018; 5 – 2019; 6 – 2020
*a – Arctic; b-a – boreal-Arctic, w – widespread (subtropics to Arctic)

No signs of borealization of fauna have been indicated by the seriation analyses.

2.5. Discussion

2.5.1. Shallow water communities of the Pechora Bay (published in Gebruk et al., 2019)

Low biomass and richness macrobenthos in the estuarine environment of the Pechora Bay were clearly different from the richer biomass and number of species marine communities of Vaigach Island, as previously found (Denisenko et al., 2003; Kucheruk et al., 2003; Denisenko S. et al., 2019). Estuaries are typically characterised by lower biodiversity, biomass and abundance of macrobenthic invertebrates compared to marine environments (Whitfield et al., 2012; Denisenko N. et al., 2019). The proportion of marine, estuarine and freshwater species in the composition of estuarine macrozoobenthos typically depends on the salinity of a particular site (Whitfield et al., 2012). The Pechora Bay is characterised as a mesohaline zone with low species richness (Denisenko N. et al., 2019). However, species richness in the area is affected more by granulometric sediment structure than organic matter content of sediments or water salinity variations within the Pechora estuary (Denisenko N. et al., 2019). In the present study fauna was comprised of marine species with few brackish crustaceans. At least one brackish species was present at each sampling site (*M. affinis* and *S. entomon*, occurred with the frequency of 0.38 and 0.25 across all sampling sites respectively).

Kucheruk et al. (2003) has previously suggested that the near-shore shallows of the Pechora Sea are unsuitable for macrobenthos due to harsh environmental conditions, namely wave action and ice cover, and macrobenthos can only be found from the water depth of 2–5 metres near Vaigach Island and from 5 metres for the rest of the Pechora Sea. Outcomes of the present study prove that the inner bay of the Russky Zavorot peninsula sheltered from the waves is suitable for in-fauna macrobenthos even in the first 1–2 metres of depth. All studied sites were characterised by muddy-sand substrates. The observed community can be interpreted as a reduced richness and biomass form of the *L. balthica*-community, described by Denisenko N. et al. (2019) from the central and northern parts of the Pechora River estuary. At the periphery of its distribution, the community is attributed to sea ice thickness and freshwater impact and therefore would seem to be comprised of eurythermal and euryhaline species. Species occurring in the shallows but not found in deeper habitats described by Denisenko included Chironomidae Gen.sp., *L. cirrata*, *S. armata* and *Y. hyperborea*.

In the Arctic intertidal and upper sublittoral zones, the sea ice thickness and under-ice freshwater impact are commonly thought of as key factors driving macrozoobenthos abundance and distribution (Ellis, 1995; Kucheruk et al., 2003; Mokievsky et al., 2016). Therefore, reduction of the sea ice volume would likely improve conditions and habitat availability for the *L. balthica*-community. To achieve a broader understanding of the biomass trends of *L. balthica* stock in Nenetsky State Nature Reserve near-shore areas, the present study can be considered as a baseline with further regular observations required.

2.5.2. Macrobenthos in the foraging grounds of Atlantic walrus near Vaigach Island (published in Gebruk et al., 2021)

In the research area near Vaigach Island the most extensive survey of macrobenthos was conducted in 2016 at 20 sampling sites to address the state of macrobenthos as well as characterise feeding resources available for benthic predators in the area. Macrobenthos within walrus feeding grounds were formed by a highly heterogeneous community of bivalves *A. borealis* – *C. ciliatum* with variable dominants and subdominants at each sampling site (mean biomass of 222.06±229.02 g/m^2 and mean abundance of 370±14 ind./m^2). These results show similarities with the most recent benthic survey at nearby Dolgy and Matveev islands, where authors described five types of macrobenthic communities mainly dominated by bivalves, with the most extensive community dominated by *A. borealis* and *M. calcarea* (Denisenko D. et al., 2019). However, the list of the dominant species identified by Denisenko was slightly different form the dominant species identified near Vaigach Island by the present study: *M. edulis*, *Mya pseudoarenaria* Schlesch, 1931, *S. groenlandicus*, *Semibalanus balanoides* (Linnaeus, 1767), *B. balanus*, *M. calcarea*, *Hyas coarctatus* Leach, 1815, *P. hyperborea* and *Buccinum undatum* Linnaeus, 1758. Only two of these species, *S. groenlandicus* and *M. calcarea*, appeared in the list of dominants in the present study.

According to the review of macrobenthos of the Pechora Sea by Denisenko (2013), the research area falls into the zone where the community *S. typicus* – *A. borealis* alternates with the community *S. groenlandicus*. However, only one sampling site of this survey was located within the research area, hence it is not surprising that more dense sampling in the present study revealed a highly mosaic community with different dominants. Remarkably in the present study *A. borealis* and *S. groenlandicus* remained in the list of dominants, whereas *S. typicus* was still present in the area with 10% occurrence across our sampling sites but did not form a large enough stock to be recognized as one of the dominants in biomass. It was previously discussed in the literature that a significant reduction of biomass of the stenothermal species *S. typicus* is the most common trend in the Russian Arctic and could either be a result of climate change or different approaches to quantifying organisms in the samples (Zhirkov, 2001).

Overall, macrobenthos with a mean biomass of 222.06±229.02 g/m^2 was available for walruses in 2016 in the research area, based on grab sampling. Previous diet studies showed that bivalves were the predominant prey items of Atlantic walruses (Gjertz and Wiig, 1992; Fisher and Stewart, 1997; Born et al., 2003). It can therefore be speculated that bivalve molluscs, *A. borealis*, *C. ciliatum* and *A. montagui,* formed the bulk of the foraging biomass available for walruses in the area. The study area likely constitutes an important feeding ground for the walruses, however the system of protected areas that is currently in place in the Pechora Sea was developed based on land-sourced data and important factors such as distribution and biomass of benthic foraging resources were not taken into consideration.

2.5.3. Temporal variation of macrobenthos in the Pechora Sea

During the six years of observations the mean biomass and community structure (expressed as relative fractions of relative production of each species to mean relative production per sample) did not significantly vary between years. The highest mean biomass was registered in 2016 (mean per sample 222.06±229.02 g/m^2) and the lowest in 2015 (44.63±54.51 g/m^2) with highest abundance in 2020 (2658±1137, ind./m^2) and lowest in 2016 (638±492, ind./m^2). According to the outcomes of PERMANOVA analysis, interaction of the year of sampling and location of sampling site contributed most to variation of macrobenthos, whereas the effects of sampling gear (the benthic grabs of two capture sizes) were negligible. This can be explained by significant spatial variation of macrobenthos previously shown in literature (Denisenko et al., 2003; Kucheruk et al., 2003; Denisenko S. et al., 2019). Overall, the community of macrobenthos can be characterised as *A. borealis – C. ciliatum*. Differences between the years can be attributed to different proportions of these (sub)communities in the sampling whereas the overall list of dominants remained the same. SIMPER analyses (Table 2.4-7) demonstrated that large species with low abundance (bivalves, gastropods and echinoderms) assure differences in mean biomass, whereas small and abundant polychaete species contribute to differences in mean abundance. To balance contributions from all groups of macrobenthos, relative production matrix was used in analyses of interannual variability of community structure, calculated as approximated relationship between biomass and abundance using formula by Clarke and Warwick (2001) based on average exponent of annual production on body-size for macrobenthic invertebrates.

The biomass of key prey items can be used as an indicator parameter of foraging capacity of the area in future studies. Specifically, in the research area near Vaigach Island six species of bivalve molluscs contributed the most to overall biomass, but also to differences observed between the years of sampling in 2015–2020, namely: *A. montagui*; *A. borealis*; *A. crenata*; *S. groenlandicus*; *C. ciliatum*; *M. calcarea.* It is difficult to estimate whether macrobenthos in the area provides enough foraging biomass to sustain the observed populations of benthic predators. To reveal impacts of impacts of increasing numbers of benthic predators in the area as well as increasing water temperature (Denisenko S. et al., 2019), further estimations of macrobenthic biomass and its dynamics are needed in the area of feeding grounds of walruses. Establishing a long-term environmental monitoring programme to observe dynamics of biomass along with walruses' behaviour and density would provide foundation for the kinds of ecosystem-based approaches needed to improve Pechora Sea resource management and to underpin Russia's nascent marine spatial planning initiatives.

It has been repeatedly predicted in the literature that increasing temperatures in the Arctic will affect benthic communities, which could lead to changes in species distribution and interaction, allow the introduction of new species, and enable decrease of arctic species alongside the increase of boreal species in the composition of benthic fauna (Lambert et al., 2010; CAFF, 2013; Renaud et al., 2015). The Barents Sea has been identified as a hotspot for "Atlantification" of seawater and the expansion of boreal species (Renaud et al., 2015; Vihtakari et al., 2018). It is likely that effects of climate change on macrozoobenthos of the Pechora Bay will appear in the foreseeable future, however no effects of borealization or Atlantification of fauna were observed in the research area during the six years of sampling. The faunal composition remained relatively stable with strong predominance of boreal-Arctic species. Seriation analyses revealed that 3% of species appeared in the last three years of sampling that have not been registered before, and 6% of species were only registered in 2015–2016, however both "new" and disappeared species are mostly boreal-Arctic. Both appearing and disappearing species comprise a combination of Arctic, boreal-Arctic and widespread species with a strong predominance of boreal-Arctic fauna. Hence, no evidence of borealization can be observed in the research area during the sampling period. One interesting observation from the seriation analyses is that two astartid bivalves, *A. eliptica* and *A. montagui,* were not found in samples from the last three years, while a closely related species from the same genus, *A. crenata,* appeared in the samples (Table 2.4-9). This suggests possibly species replacement; however, all three species are classified as boreal-Arctic, so this should not be interpreted as evidence of "Atlantification".

According to biogeographical borders in the Barents Sea (CAFF, 2013), the Pechora Sea corresponds to a transitional zone between the Atlantic boreal and the Arctic regions. Although different authors argue the exact location of the borders between biogeographical zones in the Barents region (Spiridonov et al., 2011; Mironov, 2013; Zhirkov, 2013; Shishkin et al., 2020), it is in general agreement, that the Pechora Sea corresponds to the transition zone where boreal and Arctic species coexist. Denisenko in his review (2013) showed that 70% of macrobenthos of the Pechora Sea are boreal-Arctic species, 11% boreal (Atlantic), 15% Arctic and 5% widespread species. Results of the present study in general agree with these data.

2.5.4. Key drivers of long-term change in macrobenthos

Biogeographical zonation in the Arctic in general is related to the movement and dynamics of the water masses (CAFF, 2013). Specifically, in the Barents Sea the inflow of the Atlantic water has major hydrological and climatic influence on the distribution of species (CAFF, 2013; Shishkin et al., 2020). Both research areas (Vaigach Island and the Pechora Bay) are geographically isolated from all major currents in the Pechora Sea and therefore are less influenced by fluctuations in the inflow of Atlantic waters (Figure 1.2-2). The Pechora Bay research area could be affected by the dynamics of the continental run-off through riverine input of the Pechora River, but time series data are needed to observe these dynamics.

Long-term dynamics of climatic conditions in the Barents Sea are based on the Kola Section measurements and expressed using the climate index, an approximation of mean values of air temperature, water temperature and ice-free area normalised by standard deviations (Boitsov et al., 2012). Based on the variation of the climate index in the 20th century (Figure 2.5-1), long-term climatic dynamics in the Barents Sea are described as alterations between cold and warm periods with an overall increasing trend and the latest warm period (starting from the 1990s) having the highest rate of temperature increase (Anisimova et al., 2011; Boitsov et al., 2012; CAFF, 2013). The graph of long-term dynamics of the climatic index (Figure 2.5-1), shows a period of temperature fluctuations can be approximated as 25–35 years, it is therefore evident that long-term observations are needed to observe any response to these trends in macrobenthic communities.

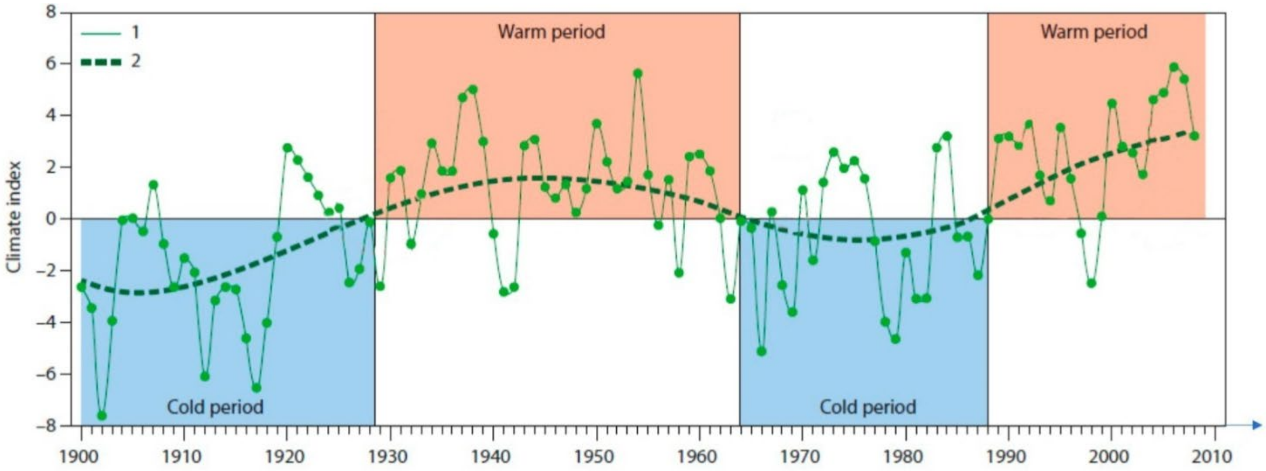


Fig. 2.5 - 1. Long-term dynamics of climatic index in the Barents Sea (1) With mean curve (sixth degree polynomial approximation); (2) Warm and cold periods represented by red and blue colours, respectively. From CAFF, 2013, based on Anisimova et al., 2011; Boitsov et al., 2012.

Aside from the climatic dynamics, influence of Atlantic waters and riverine input, direct anthropogenic pressures and biological interactions can play an important role in dynamics of macrobenthos in the Pechora Sea (Sukhotin et al., 2019). The role of benthic predators and specifically the trophic niche of the invasive benthic decapod *Chionoecetes opilio* is discussed in Chapter 3. It has been shown for Baydaratskaya Bay in the Kara Sea that Arctic macrobenthic communities that were earlier considered as stable after reaching certain threshold of anthropogenic disturbance (in that case caused by the underwater pipeline construction and related dumping of dredged sediments) can experience biodiversity loss and ecological shifts (Kokarev et al., 2015). In the research areas of the Pechora Sea dynamics of macrobenthic communities work has not currently found evidence of anthropogenic disturbance, but the long-term consequences of increasing activities of offshore industries in the region including shipping and tourism remain unknown.

2.6. Recommendations for ecological monitoring

Key recommendations for long-term ecological monitoring of macrobenthic communities in the Pechora Sea based on the outcomes of this chapter include:

To understand dynamics and cumulative impacts of stressors on Arctic benthic biodiversity, **long term monitoring** of macrobenthic communities is required. Standardised framework of data collection specifying number and locations of sampling sites, sampling gear, analysed parameters and target species is essential to ensure data compatibility.

More specific recommendations:

- To observe state of macrobenthic communities in the foraging grounds of Atlantic walruses in the Pechora Sea long-term monitoring should integrate biomass, abundance and species composition data.
- Standardised protocol for biomass measurement is essential, and it is recommended to include wet mass, dry mass and ash-free dry mass (AFDM) into the protocol where possible.
- A spatially nested design of sampling sites should be considered in the future development of monitoring framework to add additional spatial scale and increase analysis power.
- Voucher specimens should be kept for more robust cross checking, and preservation suitable for multi locus genetic studies.
- Additional environmental data collected alongside macrobenthic samples should include CTD casts for the water column and primary production measurements.
- Toxicology tests are recommended for key prey items to monitor pollution of walrus foraging recourses.
- Time series comprising minimum of 25-years of data collection is required to assess dynamics of macrobenthos against the dynamics of climatic index of the Barents Sea.
- Specific recommendations for Vaigach Island research area: (1) sample size - minimum 5 sites, (2) sampling gear – benthic grab with a 0.1 m^2 sample area (*Van-Veen* and *Okean-0.1*) with a minimum of 3 replicates each; (3) target species and parameters – the biomass of *A. borealis, C. ciliatum* and *A. montagui* as an indicator of foraging capacity of walruses. For indicator species, it is also recommended to include morphometric indices and reproductive status monitoring for population assessment.

2.7. Summary

Macrobenthos has an integral role in marine ecosystems of the Pechora Sea sustaining populations of benthic predators including the Atlantic walrus and sea ducks. However, the existing framework of protected areas does not currently consider the state of macrobenthos. Furthermore, the protected area established on Vaigach island to safeguard key haul-out and breeding sites does not extend to nearby water areas that contain key foraging grounds of benthic predators. Improved understanding of the state and dynamics of benthos is vital to improving the marine spatial planning in the area. Macrobenthos of the Pechora Sea has been studied for nearly a hundred of years, but the collected data remain fragmentary and shallow water benthos are particularly underrepresented. This study focuses on two research areas – one in the continental shallows of the Pechora Bay and another in the foraging grounds of walruses near Vaigach Island, providing new data characterising the state and variability of macrobenthos.

The Pechora Bay macrobenthos consisted of a monodominant community of *Limecola balthica* with low biomass and species richness. Paucity of macrozoobenthos was likely attributed to extreme environmental conditions in the margins of its distribution. Previous studies reported that the shallow metres of the near-shore shallows of the Pechora Sea were not suitable for development of macrobenthos (Kucheruk et al., 2003), however the present study revealed a reduced in biomass community comprised of (presumed) eurythermal and euryhaline species.

Research area near Vaigach Island was characterised by a highly heterogeneous macrobenthic community of 184 taxa overall dominated by *Astarte borealis-Ciliatocardium ciliatum* community with a mean biomass of 217.48±200.49 g/m^2. In the six years of observations, macrobenthos near Vaigach Island showed relative stability with no clear trends observed for biomass, abundance, relative production and species composition and no significant differences in mean values of abundance and biomass observed in the last four years of sampling. However, this is likely explained by the relatively short observation time and high spatial heterogeneity. Long-term cumulative impacts of changing environmental conditions, penetration of non-indigenous species (including invasive benthic omnivore, the snow crab *Chionoecetes opilio*) and anthropogenic disturbance remain uncertain and require further investigation. The biomass of key prey items, including *A. borealis*, *C. ciliatum* and *Astarte montagui*, can be used as an indicator parameter of foraging capacity of the area in future studies.

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Chapter 3. Trophic niche of the non-indigenous decapod *Chionoecetes opilio* in benthic ecosystem of the Pechora Sea

Chapter focus

Chapter 3 looks at the role of the non-indigenous benthic decapod, the snow crab *Chionoecetes opilio*, in trophic web of the Pechora Sea. In the introduction, effects of biological invasions on marine trophic webs are reviewed, and the invasion of *C. opilio* in the Barents Sea addressed. The diet of *C. opilio* in the Pechora Sea was studied through the stomach content analyses and compared to the diets of native benthic decapods. Occurrence of *C. opilio* in the research area was assessed using footage from remotely operated underwater vehicles. A conceptual diagram of trophic interspecies interaction was suggested and discussed.

3.1. Abstract

The snow crab *Chionoecetes opilio* is an important non-native commercially harvested benthic omnivore in the Barents Sea that was likely brought to the area with the ballast waters in 1990s, but its trophic niche and long-term ecosystem consequences of introduction are poorly understood. The goal of this chapter was to assess the role of *C. opilio* in the marine ecosystems of the Pechora Sea through (1) quantifying temporal change in the observed populations of *C. opilio*; (2) characterising diet of *C. opilio* and determining whether there is a potential trophic overlap with the native benthic predators.

Analyses of underwater video footage obtained using remotely operated vehicles in the Pechora Sea in 2016 and 2020 revealed growing presence of *C. opilio* in the vicinity of important foraging grounds for Atlantic walruses. Analysis of 16 video recordings (8–22 min) obtained in 2016 and eight recordings from 2020 (5–10 min) showed presence of *C. opilio* (occurrence 0.006±0.007 ind./min in 2016 and 0.012±0.011 ind./min in 2020; relative proportion 0.14±0.11 in 2016 and 0.23±0.25 in 2020), however further observations are needed to assess population dynamic.

To assess the potential for trophic overlap of *C. opilio* with native crab species, the stomach contents of three decapod species from the Pechora Sea were analysed. Specimens were collected during RV *Kartesh* expeditions in 2017–2018 with the bottom trawl *Sigsbee* (frame width 1.5 m). These included the snow crab *C. opilio* (n=23), the spider crab *Hyas araneus* (n=9) and the hermit crab *Pagurus pubescens* (n=43). Visual morphological identification of the prey items was combined with the food lump characteristic and followed by enzymatic digestion to distinguish organic debris from synthetic polymers (microplastics). Twenty categories of prey items were

identified with the most frequently occurring bivalve molluscs (*Ciliatocardium ciliatum*, *Ennucula tenuis* (Montagu, 1808), *Macoma calcarea*), polychaetes, crustaceans and plant debris. Overlapping diets of the three species suggest that *C. opilio* has the potential to compete for food resources with both *H. araneus* and *P. pubescens* (Pianka's overlap measure *C. opilio-H. araneus*=0.97; *C. opilio-P. pubescens*=0.75). Microplastics were found to be a likely stressor on this ecosystem, as 28% of all stomachs of all three species contained microplastics among prey items. None of the male *C. opilio* from the trawls reached maturity according to the discriminant morphometric function (Y=0.7–0.9), suggesting that the area is likely used as nursery grounds for smaller specimens. Conceptual diagram of trophic interspecies relationship between benthic predators and macrobenthic communities in the Pechora Sea was generated. Long-term studies of benthic ecosystem structure and functioning are now needed to more fully understand the extent to which the new competitor *C. opilio* may alter the future biodiversity of the Pechora Sea alongside the additional stressor of ingested plastics.

3.2. Introduction

The snow crab *Chionoecetes opilio* is a non-indigenous species (NIS) in the Barents Sea, first recorded in the fisheries by-catch in 1996 (Kuzmin et al., 1998). Thereafter, it appears to have formed a self-sustaining population that is predicted to further increase in numbers (Jørgensen and Spiridonov, 2013; Mullowney et al., 2018) making it an invasive species. *C. opilio* are benthic omnivores (Squires and Dawe, 2003; Zalota et al., 2018) and therefore their presence in the Pechora Sea poses a potential threat to benthic habitats and biodiversity including in the foraging grounds of listed species such as Atlantic walrus *Odobensus rosmarus rosmarus*. No information on the diet of the *C. opilio* in the Pechora Sea were available prior to this study, and the trophic relationship between *C. opilio* and other Pechora Sea benthic predators (native decapods, the Atlantic walrus and sea ducks) remain unclear.

3.2.1. Effects of biological invasions on trophic webs

Biological invasions in marine ecosystems

Invasive ecology is a relatively new field, greatly influenced by the Charles Elton's book "*The ecology of invasions by animals and plants*" (1958), that remains the most cited information source in invasion ecology (Richardson and Pysek, 2008). There is still much inconsistency in the use of terminology in literature, including the concepts of *non-native*, *alien*, *non-indigenous*, *naturalized*, and *invasive* species versus *native* species. Alien species are defined as species that were brought to a new region outside their natural distribution range as a result of human activities and the term *alien* is seen as a synonym of *non-indigenous*, *non-native*, *introduced*, *adventive*, *exotic* and *foreign* (Richardson et al., 2011). The term *naturalized* refers to an alien species with self-sustaining populations (Richardson et al., 2011). The term *invasive* is typically used to refer to species that spreads to cause an impact in the recipient ecosystem. However, the connotation of the impact can be different, and while the International Union for Conservation of Nature (IUCN) and CBD both imply that alien invasive species have negative impacts on ecosystems, biodiversity and economy, the definition based on ecological and evolutionary theory explains invasive species as an alien species that has a self-sustaining population with reproductive offspring and potential for further spread (Colautti and Richardson, 2009; Richardson et al., 2011). To minimise discrepancy in this thesis the term non-indigenous species (NIS) is used to refer to species observed outside of their recent natural distribution range, and the term invasive refers to species that either show negative impact on recipient ecosystems or massive proliferation followed by an uncontrolled spread outside the natural distribution range.

Rapid growth in offshore human activities in the recent history led to the re-distribution and anthropogenic introduction of species to new regions at the highest rate compared to any other period in the history of humankind (Riccardi et al., 2013). Invasive species from different taxonomic groups have been reported in most of the regions of the World's Ocean (Sakai et al., 2001; Gucu, 2002; Javidpour et al., 2006; Kideys et al., 2008; von der Meden et al., 2008; Braga et al., 2021). Effective control and forecasting of biological invasions are the priorities of conservation science and management. Since 2004, the International Maritime Organization (IMO) has adopted the International Convention for the Control and Management of Ships' Ballast Water and Sediments (BWM, 2004) aimed at control of invasive aquatic species. However, biological invasions in marine ecosystems remain a significant problem since many species have already been introduced to the new environments through shipping before regulations came into force, and in addition, new vectors of species redistribution continue to appear including floating plastic litter (reviewed in Avio et al., 2017).

Biological invasion is a staged process, but not necessarily linear, where species can progress to the next stage after passing through certain ecological filters or thresholds (Catford et al., 2009). Stages of invasion are typically described as: (1) transport; (2) introduction; (3) colonization; (4) naturalization; (5) spread; (6) impact (Catford et al., 2009). However, it can be argued that the impact of invasive species can occur through all stages and be pronounced on different levels

(Riccardi et al., 2013). Sokolov et al. (2016) (following Karpevich, 1975; Karpevich and Gorelov, 1995) described the theoretical establishment curve of an invasive species (Figure 3.2-1) in five phases along a naturalization-invasion continuum:

I. An introduction and adaptation period that lasts until the first reproduction cycle in the new environment;
II. A lag period is observed as the population gradually increases in number before the exponential growth;
III. An exponential increase phase;
IV. A decrease (typically driven by high mortality or lack of feeding recourses);
V. The final phase of naturalization and establishment of an invasive self-sustaining population.

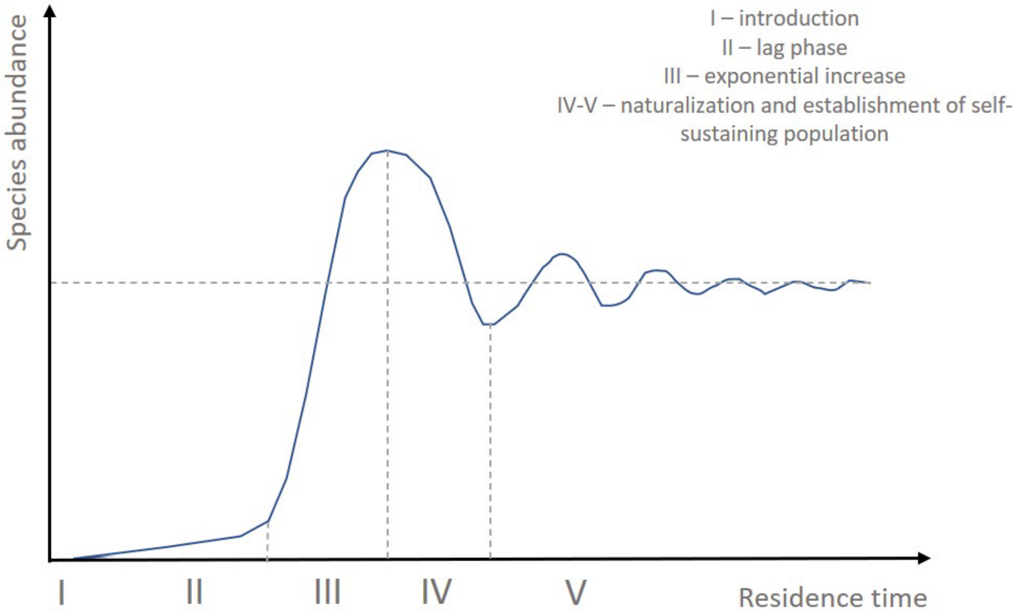

Fig. 3.2 - 1. Theoretical establishment curve of an invasive species in aquatic ecosystems (based on Karpevich, 1975; Karpevich and Gorelov, 1995; Sokolov et al., 2016).

Impacts of NIS on the recipient marine food webs

Impacts of an invader on biological communities can vary greatly (Sakai et al., 2001; Riccardi et al., 2013). Negative impacts of NIS include reduced genetic variation, eradication of native and endemic species, alteration of habitats and ecosystem services, economic loss to fisheries and other industries, ecological shifts and biodiversity loss (Wallentinus and Nyberg, 2007; Hulme et al., 2008; Molnar et al., 2008; Vilà et al., 2010). The level of impact of an NIS on an ecosystem is directly linked to its role in the trophic web in conjunction with its population size and spread (Power et al., 1996; Thomsen et al., 2014). Some researchers suggest that ecosystems characterised by low biodiversity are more vulnerable to biological invasions as the structure of the trophic web in these systems can be easily disturbed by alien species (Kennedy et al., 2002; Stachowicz et al., 2002). This effect can be also described by an insurance hypothesis (Frid, 2011), explained in Chapter 2, which suggests that species-rich systems are more resilient to external perturbations as impacts can be buffered in complex food webs. Niche-based hypotheses argue that greater impacts are expected from the NIS that have niche overlap with indigenous species and outcompete them (reviewed in Riccardi et al., 2013). Alternatively, species that occupy seemingly "empty niches" by utilising previously unused resources can become very successful (Riccardi et al., 2013).

3.2.2. Invasion and trophic role of *C. opilio* in the Pechora Sea

Invasive decapods in the Arctic

Decapod crustaceans are one of the most common groups of NIS in marine ecosystems after fish and molluscs (Zalota, 2017). However, in the Arctic region, invasive alien species are relatively rare, which could partly be attributed to historically lower shipping densities and other human activities, but also to the lack of data (CAFF, 2013). Most records of Arctic alien invasive species are terrestrial plants (e.g., the Nootka lupin *Lupinus nootkatensis* Donn ex Sims in Iceland and Greenland; furthermore, up to 15% species of the flora in Svalbard and up to 7% of plant species in the entire Arctic flora classified as non-native (CAFF, 2013). Amongst marine species, perhaps the best-known case of an invasive alien species in the Arctic Ocean is the red king crab *Paralithodes camtschaticus.* This was brought to the Barents Sea in the 1960s from the northern Pacific to establish a new fishery. After its introduction, the species successfully settled and expanded northeast and west into Norwegian waters from its area of introduction in the Murmansk Fjord (Jørgensen and Primicerio, 2007; Oug et al., 2011; Fuhrmann et al., 2015). Since the establishment of the commercial fishery, there have been significant concerns that the expansion of the crab poses threats to biodiversity and habitats and to other fisheries through impacts on benthic ecosystems (Falk-Petersen et al., 2011). Specifically, it has been shown for fjordic lagoons of the Varanger fjord that reduced biodiversity and biomass was interpreted to be a result of predation by the king crab (Spiridonov et al., 2020). Notably, the diet of the red king crab *P. camtschaticus* is non-specific and includes up to 170 species of benthic invertebrates according to different studies (reviewed in Zalota, 2017).

Another Arctic invasive decapod is the Atlantic rock crab (*Cancer irroratus* Say, 1817) that has been reported in Icelandic waters (Gislason et al., 2014), but there is currently no evidence of *C. irroratus* in the Barents Sea. The Arctic Biodiversity Assessment by the Arctic Council (CAFF, 2013) suggests that ongoing climate change and intensification of human activities may likely increase susceptibility of the Arctic region for invasive species. As such, it is predicted that the European green crab *Carcinus maenas* (Linnaeus, 1758), introduced to the US West Coast, has the potential to expand into sub-Arctic and Arctic waters (CAFF, 2013). Lack of data on invasive species in the Eurasian Arctic including the Laptev Sea and the East Siberian Sea could be related to lack of research in these areas (Zalota, 2017).

C. opilio in the Pechora Sea

C. opilio is a stenothermal brachyuran species broadly distributed in the northern Pacific and northern Atlantic Oceans, but in the Barents Sea, it is an alien invasive species (Alvsvåg et al., 2009; Sokolov et al., 2016; Mullowney et al., 2018; Zalota et al., 2018). The native distribution range *C. opilio* covers the North Pacific (northwards of the Aleutian Islands), the North-Western Atlantic and the Chukchi Sea in the Arctic Ocean (Zalota et al., 2019). In the Barents Sea *C. opilio* was likely introduced in the 1980–1990s and was first recorded in fisheries bycatch in the Barents Sea near Gusinaya Banka in 1996 (Kuzmin et al., 1998), thereafter forming a self-sustaining population (Jørgensen and Spiridonov, 2013; Sokolov et al., 2016; Mullowney et al., 2018). Since introduction *C. opilio* expanded to the central, eastern and northern Barents Sea water areas, and the adjacent Kara Sea (Zalota et al., 2018; Zalota et al., 2019). *C. opilio* is a cold-water species, typically inhabiting muddy sand grounds in waters 150–250 m deep in the Barents Sea (Bakanev et al., 2016). In the other Eurasian shelf Arctic seas, there is currently only one record of *C. opilio* from the border of the Laptev and East Siberian Seas (Sokolov et al., 2009).

By the 2010s the growing numbers of *C. opilio* in the Barents Sea enabled commercial fishery, which commenced in 2013 in an uncontrolled manner and since 2016 it has been regulated within the Russian EEZ with total allowable catch (TAC) issued annually. The commercial stock of *C. opilio* has been spatially and temporally monitored by the joint Russian-Norwegian Barents Sea ecosystem monitoring programme since 2004 (Bakanev and Pavlov, 2020) and in Russia *Nikolai M. Knipovich Polar Research Institute of Marine Fisheries and Oceanography* (PINRO) are producing openly accessed reports annually assessing dynamics of the stock and advising on the TAC. Average commercial size for male *C. opilio* in the Barents Sea is 111.5 mm carapace width (CW) (Bakanev and Pavlov, 2020). In the Pechora Sea, *C. opilio* is most abundant near the Yuzhny Island of the

Novaya Zemlya archipelago (Zalota et al., 2018), where water masses are influenced by cold Arctic waters from the Kara Strait (Bakanev et al., 2016; Zalota et al., 2018).

In 2019, commercially harvested biomass of *C. opilio* in the Barents Sea was estimated as 350–650 thousand tonnes and population is predicted to further grow in numbers (Bakanev and Pavlov, 2020). PINRO are also reporting the high spatial heterogeneity in distribution of *C. opilio* (Bakanev and Pavlov, 2020). Within the Russian EEZ in 2020 9840 thousand tonnes TAC was issued (with harvested stock estimated as 523 thousand tonnes) and suggested TAC for 2021 at 13250 thousand tonnes.

Several previous studies on diets of *C. opilio* were mostly conducted in Atlantic Canada (Miller, 1981; Brethes et al., 1982; Wieczorek and Hooper, 1995; Squires and Dawe, 2003), with some studies in the Pacific Arctic (Chuchukalo et al., 2011; Divine et al., 2017), the North Pacific (Tarverdieva, 1981; Nadtochiy et al., 2004), and in the Barents Sea (Manushin et al., 2016; Zakharov et al., 2018). Studies on *C. opilio* diets have all reported diverse diets with the main food items varying between locations: polychaetes and crustaceans near the northeastern Newfoundland shelf (Squires and Dawe, 2003); polychaetes and bivalves near the east coast of Newfoundland (Miller, 1981); and fish near Bonne Bay, off the west coast of Newfoundland (Wieczorek and Hooper, 1995). In this last case, authors hypothesised scavenging of discarded bait as the main foraging activity of snow crabs (Wieczorek and Hooper, 1995).

In the Barents Sea, adult males live deeper and consume more polychaetes and crustaceans dominant on bank slopes (Zakharov et al., 2018). Females and subadult males show significant consumption of molluscs dominant in shallower areas, which they mostly inhabit (Zakharov et al., 2018). Most early studies agree on polychaetes, molluscs, crustaceans and echinoderms being present in diets of *C. opilio*, but with altering frequencies of occurrence in stomachs depending on species composition of local macrobenthos (Squires and Dawe, 2003, Manushin et al., 2016; Zakharov et al., 2018).

3.2.3. Native benthic predators in the Pechora Sea

Native benthic decapods

Two species of benthic-feeding decapods that are commonly found in the Pechora Sea are the great spider crab *Hyas araneus* and hermit crab *Pagurus pubescens*. *Hyas areneus* is a benthic decapod species widely distributed in the boreal North Atlantic and adjacent Arctic seas (d'Udekem d'Acoz, 1999). It is the most common native brachyuran crab in the Barents Sea found from the intertidal to lower subtidal zones (Kuznetsov, 1964; Zimina et al., 2015). The hermit crab *P. pubescens* is a boreal Arctic species, also common in the Barents Sea. It usually dwells in the shells of *Buccinum* spp., *Neptunea* spp. and other gastropods, and is relatively small in size, its body length not typically exceeding 100 mm (Gaevskaya, 1948; d'Udekem d'Acoz, 1999), although larger specimens are sometimes reported, for example in Western Spitsbergen (Barnes et al., 2007).

Early studies on cold-water crab feeding indicate that they are opportunistic feeders, consuming the most abundant benthic organisms, though usually one food group/species dominates their diet, and this varies regionally (Kun and Mikulich 1954; Kulichkova, 1955; Cunningham, 1969; Tarverdieva, 1981; Jewett et al., 1989).

The diets of *H. araneus* and *P. pubescens* have not been extensively studied. *H. araneus* is known as a predator, very rarely consuming food items of plant origin, but more actively feeding on a broad range of benthic, hyperbenthic and planktonic species. These include hydroids, loricates, gastropods, bivalves (including juveniles of scallops and mussels), amphipods, copepods, euphausiids, small crabs, sea stars, brittle stars, juvenile sea urchins and fishes (Squires, 1990; Arsenault and Himmelman, 1996; Fagerli et al., 2013; Pushkina, 2017). Fatty acid studies in Spitsbergen showed that *H. araneus* in that region consume mostly benthic seston-feeding invertebrates (Paar et al., 2019) and even zooplankton (Legeżyńska et al., 2014). These food sources were also indicated by stable isotope analysis of the trophic status of this species in the southern Barents Sea fjords (Zalota, 2017; Spiridonov et al., 2020).

In the Atlantic waters off Canada, *P. pub*escens is known to feed on phytobenthos, foraminifera, amphipods, ostracods, hydroids, fragments of bivalves, polychaetes and brittle stars (Squires, 1990). In the Kongsfjord of Spitsbergen (Paar et al., 2019) and the fjords of the southern Barents Sea (Zalota, 2017; Spiridonov et al., 2020), *P. pubescens* occupies a somewhat lower trophic level than *H. araneus*. There is also evidence that *P. pubescens* can consume plant material of terrestrial origin in the areas of abundant ornithogenic (bird-formed) coastal vegetation in Spitsbergen (Zmudczyńska-Skarbek et al., 2015).

Apex benthic predators

Atlantic walrus

The most abundant benthic-feeding marine mammal in the Pechora Sea is the Atlantic walrus. The Atlantic walrus *Odobenus rosmarus rosmarus* has an Arctic to sub-Arctic distribution from the eastern Canadian Arctic to the Kara Sea. The IUCN lists it as Near-Threatened (Kovacs, 2016). Despite its wide distribution, the subspecies has a relatively narrow ecological niche and only specific areas provide both appropriate haul-out sites and adequate foraging resources (Born et al., 1995). Atlantic walruses are benthic predators that predominately feed on bivalve molluscs (Born et al., 2003). In winter, walruses haul out on the sea ice, however, in summer they require terrestrial haul-out sites near feeding grounds with large areas of shallow water and suitable bottom substrata to support productive macrobenthic communities (Wiig et al., 2014). An individual adult needs a daily gross energy intake of 200 kJ per kg body mass, corresponding to 35–50 kg of feeding biomass of macrobenthos (Born et al., 2003). Walruses actively consume bottom-dwelling invertebrates, specialising on bivalve molluscs (Kastelein and Mosterd, 1989; Born et al., 2003). However, their diet can include mobile benthic crustaceans, gastropods, and other invertebrates in both the Atlantic (Svetocheva and Semenova, 2017; Denisenko et al., 2019) and the Pacific subspecies (Fisher and Stewart, 1997; Chakilev and Kochnev, 2014). In the Barents Sea, Atlantic walruses inhabit areas of Svalbard, Franz Josef Land, Novaya Zemlya and the Pechora Sea (Wiig et al., 2014). Satellite tagging of 35 walruses in the Pechora Sea from 2012 to 2017 revealed that most animals resided in the Pechora Sea throughout the whole period, likely using marine habitats between Vaigach and Matveev Islands as their key feeding grounds (Semenova et al., 2019).

Waterfowl

The Nenetsky State Nature Reserve provides nesting and feeding grounds, and forms part of the migration routes for 125 species of waterfowl and costal birds. This includes species from the red list of endangered species of the Russian Federation and IUCN red list of threatened species, such as: the yellow-billed loon *Gavia adamsii*; Bewick's swan *Cygnus columbianus bewickii*; the lesser white-fronted goose *Anser albifrons*; the red-breasted goose *Branta ruficollis* and others (IUCN, 2021). Marine ducks, including King eiders, are specialized benthic feeders and their main prey items are bivalves (Sukhotin et al., 2008). Marine ducks, including the King eider and the common scoter form summer gatherings of up to tens of thousands of individuals on Dolgy Island from mid-July to mid-October, to feed and moult before migrating to wintering grounds (Sukhotin et al., 2008). Eiders, like Atlantic walruses, are specialized benthic predators feeding on marine invertebrates and specifically bivalves (Born et al., 2003; Sukhotin et al., 2008).

C. opilio may compete with walruses for the native benthic communities, or alternatively the arrival of the crabs in the 1990s may now provide a novel foraging resource for the benthic predators. Hence, baseline research on the trophic niche of *C. opilio* in the Pechora Sea is of crucial importance.

3.2.4. Objectives and scope of this chapter

Despite growing scientific and industrial attention on the Pechora Sea, our understanding of the Pechora Sea food web and trophic relationships between species remains limited, and in particular, the extent to which the spread of *Chionoecetes opilio* may impact these relationships and alter biodiversity. The main **aim of this chapter** was to characterise the trophic role of *C. opilio* in the Pechora Sea and to suggest model of trophic interactions of the benthic predators in the Pechora Sea.

More specifically, this chapter had the following **research objectives**:

1) To quantify temporal changes in the occurrence of *C. opilio* and other decapods on walrus foraging grounds near Vaigach Island.
2) To characterise diets of the three decapod species (*C. opilio*, *H. araneus* and *P. pubescens*) and determine whether there is a potential trophic overlap. A prediction was made based on literature review from other regions where *C. opilio* competes over foraging recourses with native benthic decapods.
3) To suggest a model of trophic interactions between the benthic predators and macrobenthos in the Pechora Sea.

Decapod specimens used in this study were collected during the RV *Kartesh* expedition in 2017. Remotely operated vehicle (ROV) video archives were provided by the LMSU MRC. Both diet assessment and video analyses were conducted in the Changing Oceans laboratory in University of Edinburgh.

Diet assessment used in this study aimed to improve understanding of ecological and trophic niche of *C. opilio* in the Pechora Sea and inform future management and policy decisions leading to prevention of potential trophic shifts and biodiversity loss in the region.

3.3. Methods

3.3.1. ROV video recordings

Video recording was carried out during the RV *Kartesh* research expeditions to the Pechora Sea in 2016 and 2020, using the ROV *Super GNOM Plus* (Table 3.3-1, Figure 3.3-1). The ROV was equipped with two video cameras (*Sony Super HAD 2 CCD*) posed at a tilt of ± 50°. The ROV lighting system was synchronised with a camera (10 light-emitting diodes, 6000 Lumens each) and a navigation system with a course detector and depth sensor. A total of 16 video transects were undertaken in 2016, approximately 10 minutes each (counting from the moment the ROV reached the seafloor until the beginning of its ascent), and 8 transects in 2020. Coordinates and general characteristics of sites of ROV deployment are provided in Table 3.3-1 and Appendix 3-1.

Table. 3.3 - 1. Coordinates, water depth and duration of ROV video transects analysed in this study.

Video №	Year	Benthic site №	Video duration (minutes)	Starting coordinates (degrees, decimal minutes N; E)		Finishing coordinates (degrees, decimal minutes N; E)		Maximum water depth (m)
2016								
Video 1	2016	1	09:52	69°27.195'	058°33.672'	69°27.193'	58°33.660'	9.8
Video 2	2016	6	08:18	69°26.737'	058°09.819'	69°26.734'	58°09.814'	31.1
Video 3	2016	10	08:58	69°36.440'	058°06.223'	69°36.437'	58°06.224'	34.4
Video 4	2016	1w11	12:21	69°35.115'	058°31.236'	69°35.114'	58°31.249'	30.1
Video 5	2016	11	14:46	69°37.568'	058°55.385'	69°37.565'	58°55.396'	28.8
Video 6	2016	ROV6	11:25	69°51.470'	059°11.691'	69°51.469'	59°11.690'	9.6
Video 7	2016	1N	13:53	69°43.719'	059°25.806'	69°43.716'	59°25.803'	29.5
Video 8	2016	3N	17:23	69°42.249'	058°46.377'	69°42.246'	58°46.360'	30.7
Video 9	2016	4N	19:43	69°45.640'	058°57.334'	69°45.632'	58°57.331'	32.1
Video 10	2016	6N	22:48	69°48.647'	058°54.712'	69°48.643'	58°54.706'	40.8
Video 11	2016	10N	09:00	69°51.840'	058°54.339'	69°51.836'	58°54.312'	44.3
Video 12	2016	9N	10:53	69°50.728'	058°45.817'	69°50.729'	58°45.816'	43.7
Video 13	2016	8N	12:46	69°49.034'	058°27.680'	69°49.034'	58°27.674'	34.9
Video 14	2016	12N	14:29	69°54.414'	058°30.867'	69°54.413'	58°30.863'	37.7
Video 15	2016	11N1	16:21	69°55.629'	058°41.637'	69°55.627'	58°41.645'	69.9
Video 16	2016	11N2	18:15	69°56.819'	058°44.136'	69°56.820'	58°44.139'	50.8
2020								
Video 1	2020	4N	09:27	69°45.603’	58°57.391’	69°45.196’	58°57.049’	29.2
Video 2	2020	4N	05:04	69°45.603’	58°57.391’	69°45.196’	58°57.049’	29.3
Video 3	2020	9N	09:27	69°50.739’	58°45.842’	69°51.031’	58°45.975’	42
Video 4	2020	9N	06:58	69°50.739’	58°45.842’	69°51.031’	58°45.975’	42.4
Video 5	2020	4	09:49	69°18.656’	57°11.268’	69°18.652’	57°12.534’	27.8
Video 8	2020	11w16	09:30	69°36.469’	58°29.402’	69°36.614’	58°29.630’	29.9
Video 9	2020	11w16	09:41	69°36.469’	58°29.402’	69°36.614’	58°29.630’	29.9
Video 12	2020	6	09:47	69°31.477’	58°07.969’	69°31.451’	58°08.377’	28.9

3.3.2. Field sampling (diet analysis)

Specimens for diet analyses were collected during the RV *Kartesh* expeditions to the Pechora Sea in 2017 at two sites (9N and 4N); and in 2018 at three sites (9N; 4N; D1) using a *Sigsbee* bottom trawl with a 1.5-m wide frame and a 0.5 mm mesh (Table 3.3-2; Figure 3.3-2).

Table. 3.3 - 2. Positions of trawling sites (taken at the beginning of a transect), water depth (m) and key characteristics of macrobenthic communities: biomass (g/m^2), number of species, dominant species.

Site №	Coordinates (degrees, decimal minutes, N; E)		Water depth, m	Wet biomass, g/m^2	Number of species	Dominant species
9N	69°50.727'	58°45.804'	39	522	45	*Astarte borealis*
4N	69°45.635'	58°57.347'	28	32	49	*Astarte montagui*
D1	69°17.809’	58°30.986’	18	n/a	n/a	n/a

Trawling was conducted at 2 knots for 30 minutes corresponding to a roughly linear 2 km transect. Bottom sediments were homogeneous sands with silts across the whole sampling area. Bottom sediments from trawl catches were washed over a 0.5 mm mesh with seawater. Individuals of the decapod species *C. opilio*, *H. araneus* and *P. pubescens* were then manually extracted and preserved for further analyses. Individuals used for stomach content analysis (collected in 2017) were preserved in 4% formaldehyde solution, then dissected in the laboratory. Extracted stomachs were transferred into 70% ethanol. All crabs were weighed prior to dissecting, their sex was identified, morphometric measurements were taken with Vernier calliper and included the following: CL – Carapace Length; CW – Carapace Width, CH – Carapace Height (Depth); ChL – Chela Length; ChH – Chela Height (Depth) (Appendix 3-2; morphometric indexes demonstrated on Figure 3.3-2D). Maturity of *C. opilio* was defined using the discriminant morphometric function based on carapace width and chela height (Conan and Comeau, 1986) calculated as following:

$$Y = -0.78893 \log_e CW + 0.614488 \log_e ChH + 1.76051$$

Where Y = maturity (mature males: $Y>0$); CW = carapace width, mm; ChH = chela height, mm.

3.3.3. Data analysis

Video analyses

ROV video recordings were analysed using the open-source *VLC media player* software. All mobile benthic decapods were counted and where possible identified to the species or genus level (Figure 3.3-2B demonstrates taxonomic tagging of video footage). Occurrence (individuals per minute) of decapods on video recording was then calculated as the total number of mobile benthic decapods (including decapods not identifiable to the species level) divided by the duration of time of video transect from the moment the ROV reached the seabed until the start of ascent, excluding non-readable fragments of video recordings (i.e., where the seabed was not visible) and when the camera was stationary (Mokievsky, 2015). Pearson's *r* correlation was used to define statistically significant ($p<0.05$) correlations between macrobenthic biomass in grab samples and decapod occurrence based on ROV video recordings (to test whether crabs have a tendency to form feeding aggregations with higher density in the areas of higher biomass of macrobenthos). A series of two sample tests were used to compare the frequencies of occurrence and relative proportions of snow crab in 2008 and 2016, including the two-tailed (Wilcoxon) Mann-Whitney U test (nonparametric); Mood's median test for equal medians, Kolmogorov-Smirnov test for equal distributions (Hammer and Harper, 2006). Statistical calculations were performed using free software PAST version 3.22 (Hammer and Harper, 2006), unless otherwise specified.

Diet analyses

Seventy-five decapods were used for stomach content analyses, of which 23 were *C. opilio*, 9 were *H. araneus* and 43 were *P. pubescens*. Stomachs were dissected and their contents visually examined under a stereomicroscope (dissection diagram shown on Figure 3.3-2C). Each item was categorised into prey items (digestible remains of animals, unidentified organic debris) and inclusions. Prey items were identified to the lowest possible taxonomic level where possible. Partly digested matter with no preserved hard structures were divided into "plant debris" (remains of algae or aquatic plants with structures like blades, rhizoids) and "organic debris" (digested amorphous material, detritus). Inclusions included sand, feathers and microplastics. Microplastics were defined as non-digested fibres or particles <5 mm lengths made of firm synthetic materials, and were often brightly coloured (Avio et al., 2017) (Studied in more detail in Chapter 4).

Food lump analysis was carried out following Burukovsky (2009). For each stomach, the level of fullness was visually estimated and only stomachs that were >25% full were used for food lump reconstructions. For each item in a stomach (prey items only) the percentage volume in the food lump was visually estimated. Based on average percentage volumes a so-called "virtual food lump" (Burukovsky, 2009) was then reconstructed for each species to integrally characterise diets. Besides level of fullness and prey species composition, other indices included: (1) dominance (as percentage of stomachs where a single prey item comprised >60% of the food lump of all stomachs of species); (2) mean number of prey items per stomach for species. In addition, presence-absence prey item against each stomach matrix was constructed. Presence-absence data were used to calculate frequencies of occurrence of each stomach content component in diets of each species (as percentage of stomachs where this item was present).

To assess predicted number of species in the diet the decapods, species accumulation curves were constructed using species (diet components) richness ($\tilde{S}$) with the Chao-2 type estimator as the following:

$$\tilde{S} = S_{obs} + \frac{(H-1)s_1^2}{2Hs_1}$$

Where H refers to the number of samples (stomachs), S_{obs} refers to the total number of observed species (diet components) and S_1 refers to the number of species (diet components) found in exactly one stomach.

Pianka's overlap measure (Pianka, 1974) was used to assess overlap in feeding niches based on the frequencies of occurrence of feeding items following Krebs (1998):

$$O_{jk} = \frac{\sum_i^n p_{ij}p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

Where O_{jk} refers to Pianka's measure of niche overlap between species j and species k, p_{ij} refers to proportion resource is one of the total resources used by species j (occurrence of feeding item); p_{ik} refers to proportion resource is one of the total resources used by species k; n refers to the total number of resources (feeding items).

To assess relationships between diets of the three species in more detail, I created a non-metric multidimensional scaling (nMDS) plot based on the Bray-Curtis similarity index and subsequent cluster analysis based on an unweighted pair group method using the arithmetic mean (UPGMA) algorithm. SIMPER (similarity of percentages) analyses were then carried out to assess contributions to differences between diets of different species. A pairwise analysis of similarities (ANOSIM) analysis was performed, p-values of each pair were given to ascertain statistical significance with α set to 0.05, and sequential Bonferroni corrections were applied. All statistical calculations were performed using he free statistical software *PAST version 3.22* (Hammer and Harper, 2006).

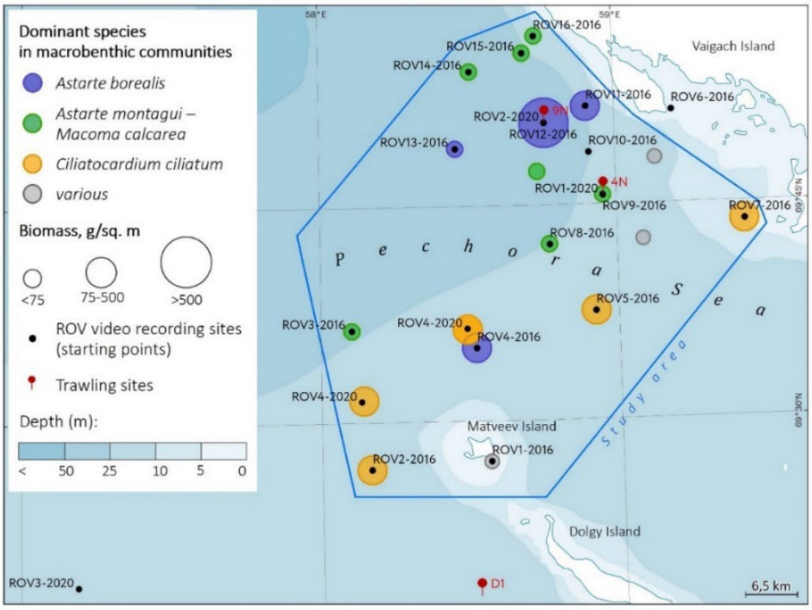

Fig. 3.3 - 1. Sampling area: trawling sites are shown with red pins; circles of different colour represent ROV sites with dominant macrobenthic species and relative macrobenthic biomass for each. Map courtesy of the LMSU MRC.

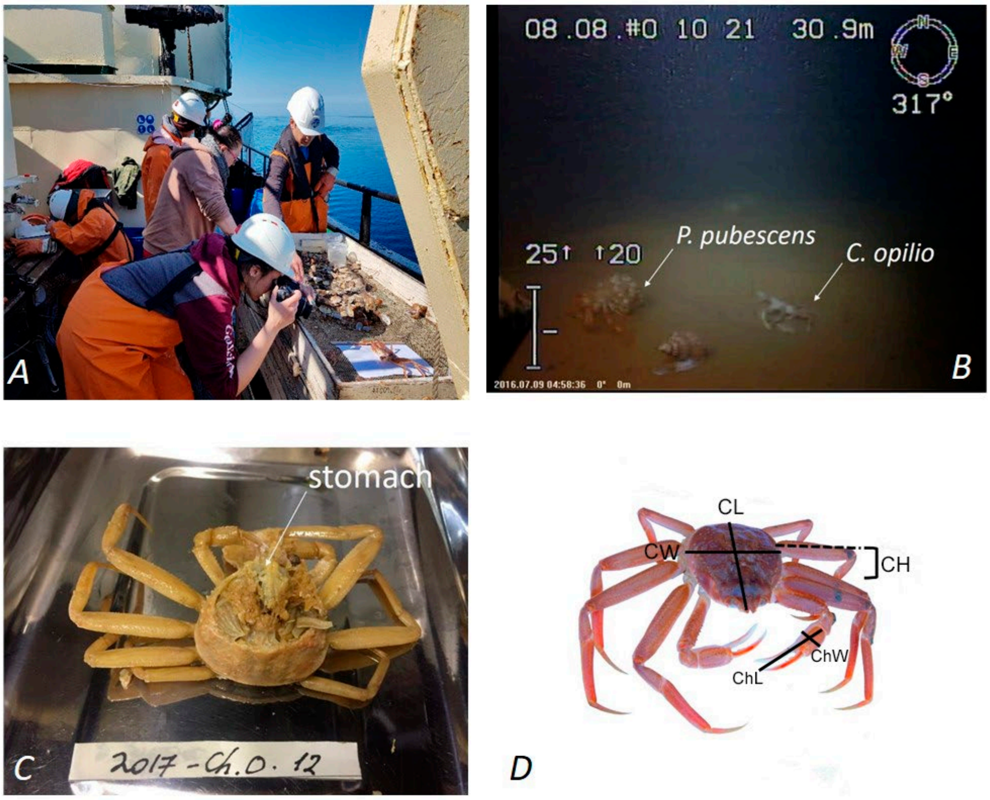

Fig. 3.3 - 2. Overview of the methods used for diet analyses: (A) Field sampling of decapods using the Sigsbee bottom trawl during the 2017 RV *Kartesh* expedition; (B) Snapshot of the ROV video recording with *C. opilio* and *P. pubescens*; (C) Dissection of *C. opilio* to extract the stomach; (D) Morphometric indices measured with the calliper (CL – Carapace Length; CW – Carapace Width, CH – Carapace Height (Depth); ChL – Chela Length; ChH – Chela Height (Depth)). Photo courtesy of the LMSU MRC.

3.4. Results

3.4.1. Occurrence of *C. opilio* in the Pechora Sea

In 2016, the following mobile benthic invertebrates were identified based on video recordings: the snow crab *Chionoecetes opilio,* the spider crab *Hyas araneus*, the hermit crab *Pagurus pubescens* and unidentified decapods. Species identification was confirmed by trawl samples taken at sampling sites 9N and 4N. A total of 255 mobile benthic decapods were recorded in video transects (Appendix 3-1). *P. pubescens* was the most abundant decapod in the area, accounting for >65% of the total number, with *C. opilio* and *H. araneus* being similarly present, accounting for ~13% each. The average decapod occurrence was 2.88±2.74 ind./min, ranging between sampling sites from 0.68 ind./min to 11.67 ind./min. Noticeably, at least one decapod was present in each recording. Values of decapod occurrence were the highest at sampling sites 11N2, 11N1 and 12N in the northeast of the research area closest to the shoreline of Vaigach Island, whilst sites 1 and 6 to the south from Matveev Island showed the lowest values. Occurrences of each species and contribution of decapod species to overall occurrence are illustrated in Figure 3.4-1. There was no statistically significant correlation between macrobenthic biomass and crab occurrence (Pearson's correlation coefficient R=-0.07; p>0.05). No positive or negative correlation were found between the occurrence of the two crab species, *C. opilio* and *H. araneus* (R=0.04, p>0.05).

In 2020, the same three species were identified in the footage: *C. opilio*, *H. araneus* and *P. pubescens.* Of which hermit crabs were the most common. The average decapod occurrence in 2020 was 4.01±3.65 ind./min ranging from 0 to 10 (Figure 3.4-1). It is important to highlight that in 2020 the general quality of video recordings was lower with a higher proportion of "non-meaningful" time where the seabed was not visible due to currents and suspended mater in water. Occurrence data for all species for both years presented in Appendix 3-1.

The mean occurrence of *C. opilio* in the video were similar in 2020 (0.012±0.011 ind./min) compared to 2016 (0.006±0.007 ind./min). The relative proportion of *C. opilio* to total amount of decapods was (0.14±0.11) in 2016 and (0.23±0.25) in 2020 (Figure 3.4-2). Statistical tests did not reveal significant differences in frequency of occurrence or relative proportion of the snow crab between the years Table 3.4-1.

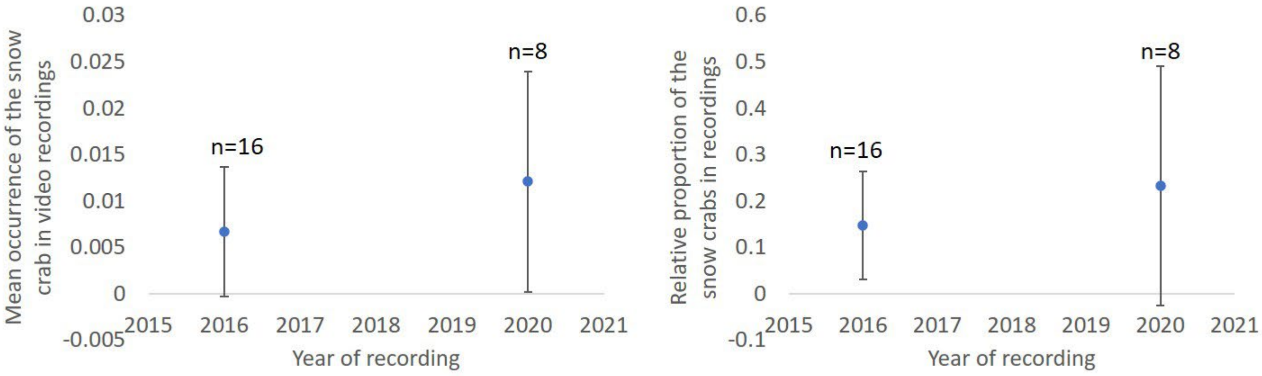

Fig. 3.4 - 1. Mean occurrence of *C. opilio* on video recordings (ind./min) on the left, and relative proportion of *C. opilio* to total number of decapods on video recordings on the right.

Table. 3.4 - 1. Statistical tests comparing medians, variance and distributions of snow crab occurrence and snow crab proportion in 2016 and 2020.

Test	**Snow crab occurrences**	**Snow crab proportion**
t test	Not applicable (normal distribution assumed)	Not applicable (normal distribution assumed)
F test for equal variances	Not applicable (normal distribution assumed)	Not applicable (normal distribution assumed)
Mann-Whitney test for equal medians	U=49.5, p=0.38; permutation N=9999	U=56; p=0.63; permutation N=9999
Mood's median test for equal medians	Chi^2=0.75, p=0.38; df=22	Chi^2=0.75; p=0.38; df=22
Kolmogorov-Smirnov test for equal distributions	D=0.5; p=0.08	D=0.25; p=0.8

Due to the small sample size (data only from two years of observations available with relatively small number of observations for each year) these outcomes should be considered as preliminary and continuing observations as well as improved protocols of data acquisition, calibration and interpretation are required for better interpretation of the dynamics of *C. opilio* population in the research are.

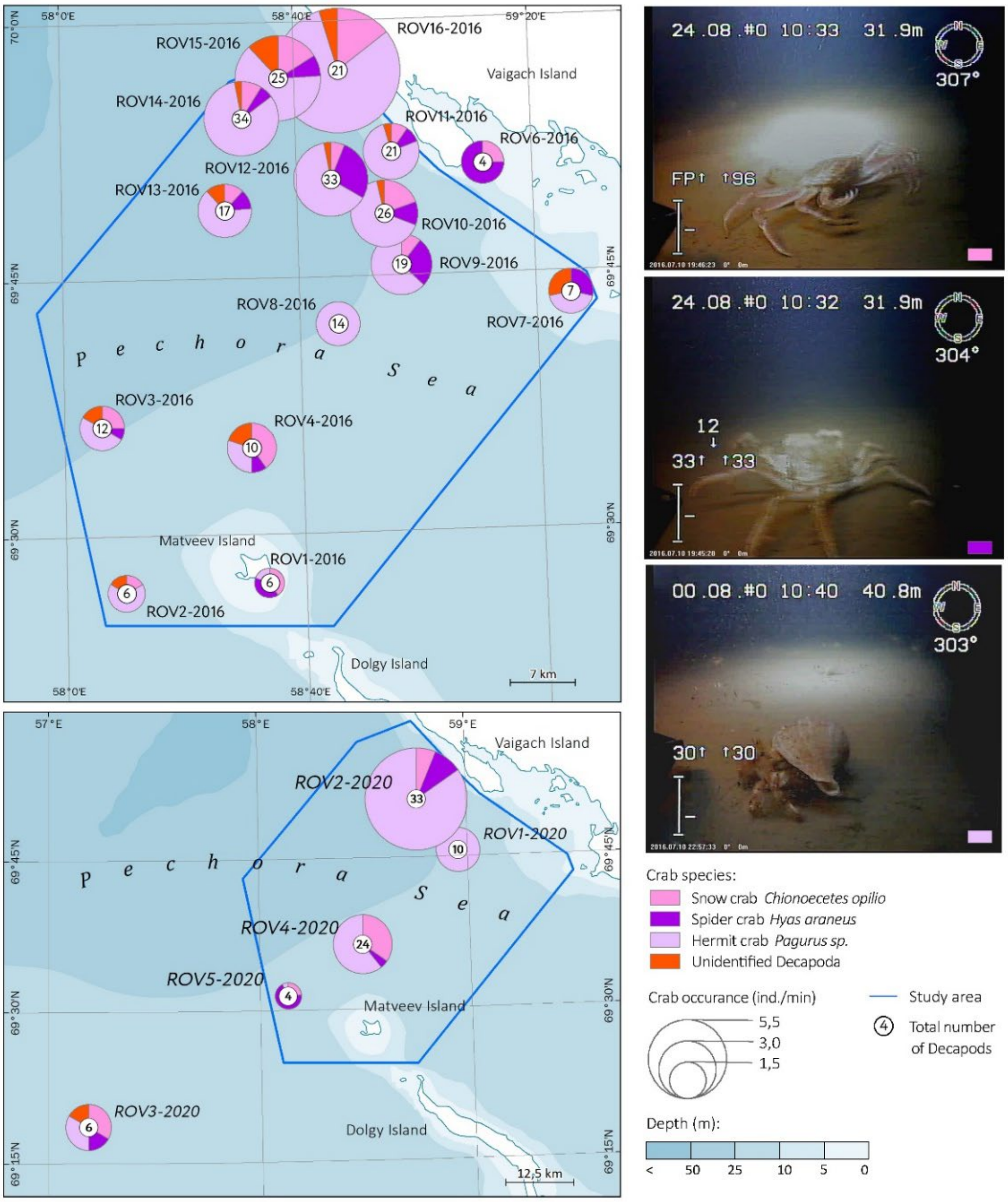

Fig. 3.4 - 2. Occurrence of benthic decapods in the Pechora Sea in 2016 and 2020. Pie charts show species composition by different colour sectors and are proportional to crab occurrence, ind./min, number in the centre shows the total sightings of decapods on each recording. Top left map published in Gebruk et al., 2021a.

3.4.2. Stomach content analysis (published in Gebruk et al., 2021b)

The crabs collected were a mixture of males and females with a predominance of males in all the three species: 13 males/10 females of *C. opilio*; 7 males/2 females of *H. araneus*; 32 males/11 females of *P. pubescens*. *C. opilio* were below commercial size (111.5 mm CW, Bakanev and Pavlov 2020). Noticeably, *C. opilio* and *H. araneus* were of a similar size group: the average *C. opilio* CL was 32.0±3.75 mm, ranging from 27 to 32 mm; the average CL of *H. araneus* was

47.0±8.44 mm (28–58 mm); and *P. pubescens* were 4–5 times smaller with a CL of 8.5±2.62 mm CL (4.0–12.5 mm). Measurements of all specimens presented in Appendix 3-2. None of the male *C. opilio* reached maturity according to the discriminant morphometric function (Conan and Comeau, 1986): Y=0.733–0.988 (mature males at Y>1).

Approximately 22% of all stomachs were empty or near-empty (<25% fullness), including two stomachs of hermit crabs (out of 43), three stomachs of *H. araneus* (out of 9) and 11 stomachs of *C. opilio* (out of 23). The rest contained prey items and were identified as full or near-full (>75% fullness) or not empty (25–75%). All stomach contents reflected mixed diets with an average of 6 prey items (5±1.8 for *C. opilio* and *H. araneus*; 6±1.2 for *P. pubescens*). Low value of dominance index (3%) showed that few food lumps were dominated by only one prey item (excluding organic debris).

Diet composition

Nineteen categories of items were identified in stomach contents, 15 of which were classified as prey items. Twenty-seven taxa of benthic invertebrates were identified (12 to species level, 5 to genus, rest to families or above). A full list of prey items is presented in Appendix 3-3. In respect to species richness, bivalve molluscs, annelids and foraminifers were the most diverse groups, accounting for 5–6 taxa each. Most of the other taxonomic groups were represented by a single species or by unidentifiable fragments. Identified bivalves included *Astarte elliptica*, *Mytilus edulis*, *Ciliatocardium ciliatum*, *Dacrydium vitreum* (Møller, 1842), *Ennucula tenuis* and *Macoma calcarea.* Identified annelids (polychaetes) included *Pectinaria* sp., *Nephtys* sp., *Owenia* sp., Maldanidae gen. sp., Cirratulidae gen. sp. and Aphroditifornia gen. sp.

The most frequently occurring prey items in food lumps, excluding organic debris, were bivalve molluscs and annelids for *C. opilio* and *H. araneus*, with plant debris for *P. pubescens* (Figure 3.4-3). Crustaceans (amphipods or barnacles) were represented in >10% of stomachs of each species, whilst frequency of occurrence of all other prey items significantly varied between the three crab species (Figure 3.4-3). Food lumps of *H. araneus* had relatively small number of prey items (6 excluding detritus and inclusions), each was present in >10% of stomachs, as opposed to *P. pubescens* and *C. opilio* that had larger variety of prey items (10–13) with altering frequencies of occurrence ranging from 2% to 83%.

Noticeably, smaller animal taxa were more frequent in stomachs of *P. pubescens* than in other decapods. Foraminifers (*Cibicides refulgens* Montfort, 1808, *Elohidium excavatum* (Terquem, 1875), *Buccella frigida* (Cushman, 1922) and others) were found in 37% of *P. pubescens* stomachs, 9% of *C. opilio* and 1% of *H. araneus*. Similarly, hydrozoans (*Obelia* sp. and others) were present in 35% of *P. pubescens*, 11% of *H. araneus* and 4% of *C. opilio.* Nematodes and ostracods were only present in stomachs of *P. pubescens*.

Sand granules were present in the majority among the inclusions of all stomachs of all species with a 92% average frequency of occurrence (ranging from 87% for *C. opilio* to 100% for *P. pubescens*). Microplastics occurred with the 28% average frequency, ranging from 22% for *H. araneus* to 35% for *C. opilio*. Organic debris appeared in all non-empty stomachs of all species (100% frequency of occurrence).

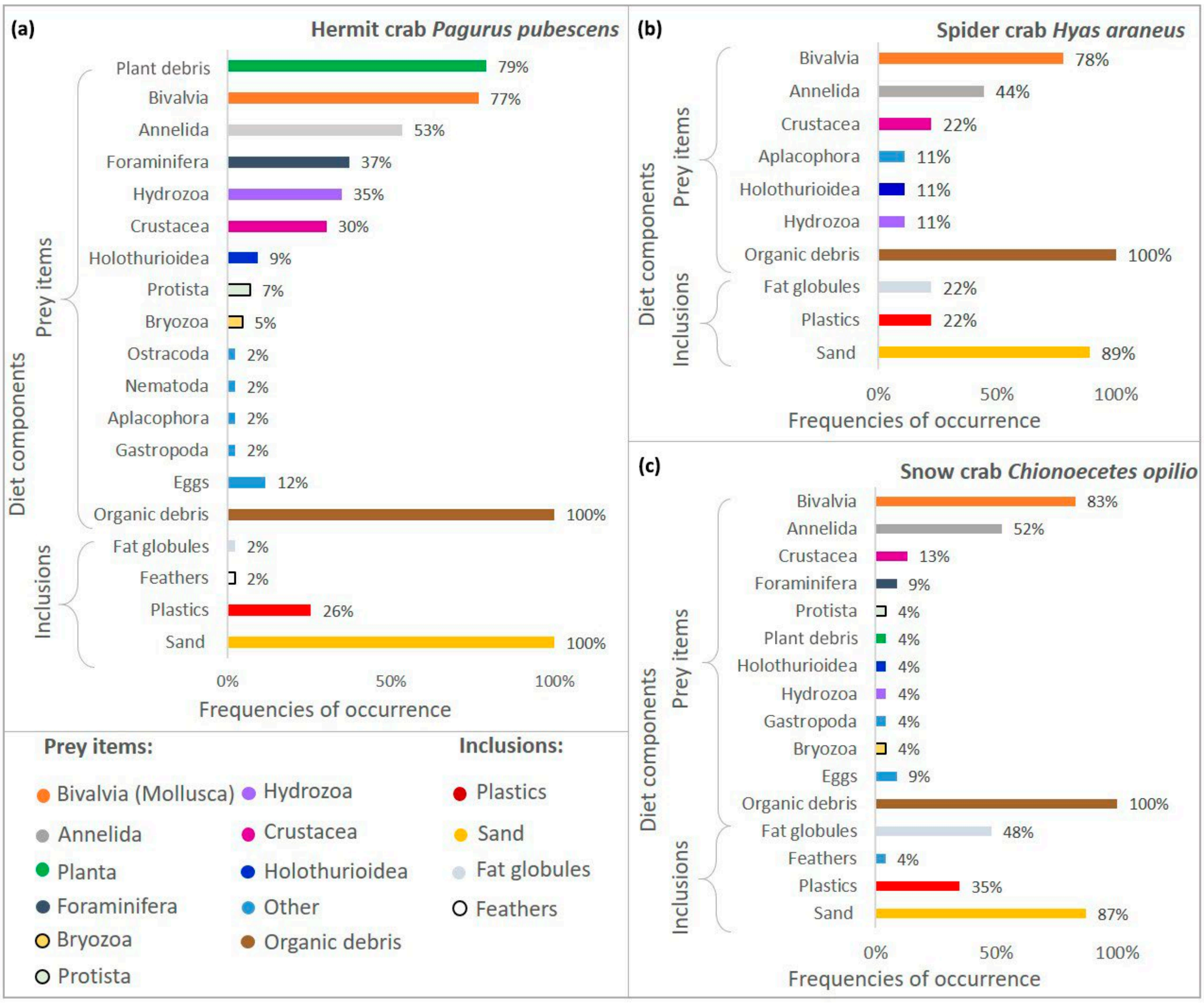

Fig. 3.4 - 3. Frequency of occurrence (%) of diet components in stomachs of (A) *P. pubescens*; (B) *H. araneus*; and (C) *C. opilio*. Figure published in Gebruk et al., 2021b.

Similarly, organic debris played an important role in food lumps of all three species (Figure 3.4-4). In the food lump of *P. pubescens*, organic debris accounted for 70% of total volume; followed by sand granules (14%), bivalve molluscs (6%), plant debris (5%), and other prey items that together only accounted for 3% of the volume. Food lump of *H. araneus*, also primarily consisted of organic debris (58% of the total volume), followed by bivalve mollusc (21%), sand granules (12%), polychaetes (7%), with minor contributions from hydrozoans (1%), and other groups (1%). On the other hand, bivalve molluscs (37%) were key contributors to the total volume of the food lump of *C. opilio* followed by organic debris (36%), sand (13%), polychaetes (5%), holothurians (5%), and other groups (together accounting for 4% of the total volume). Raw stomach content data are available in Appendix 3-4.

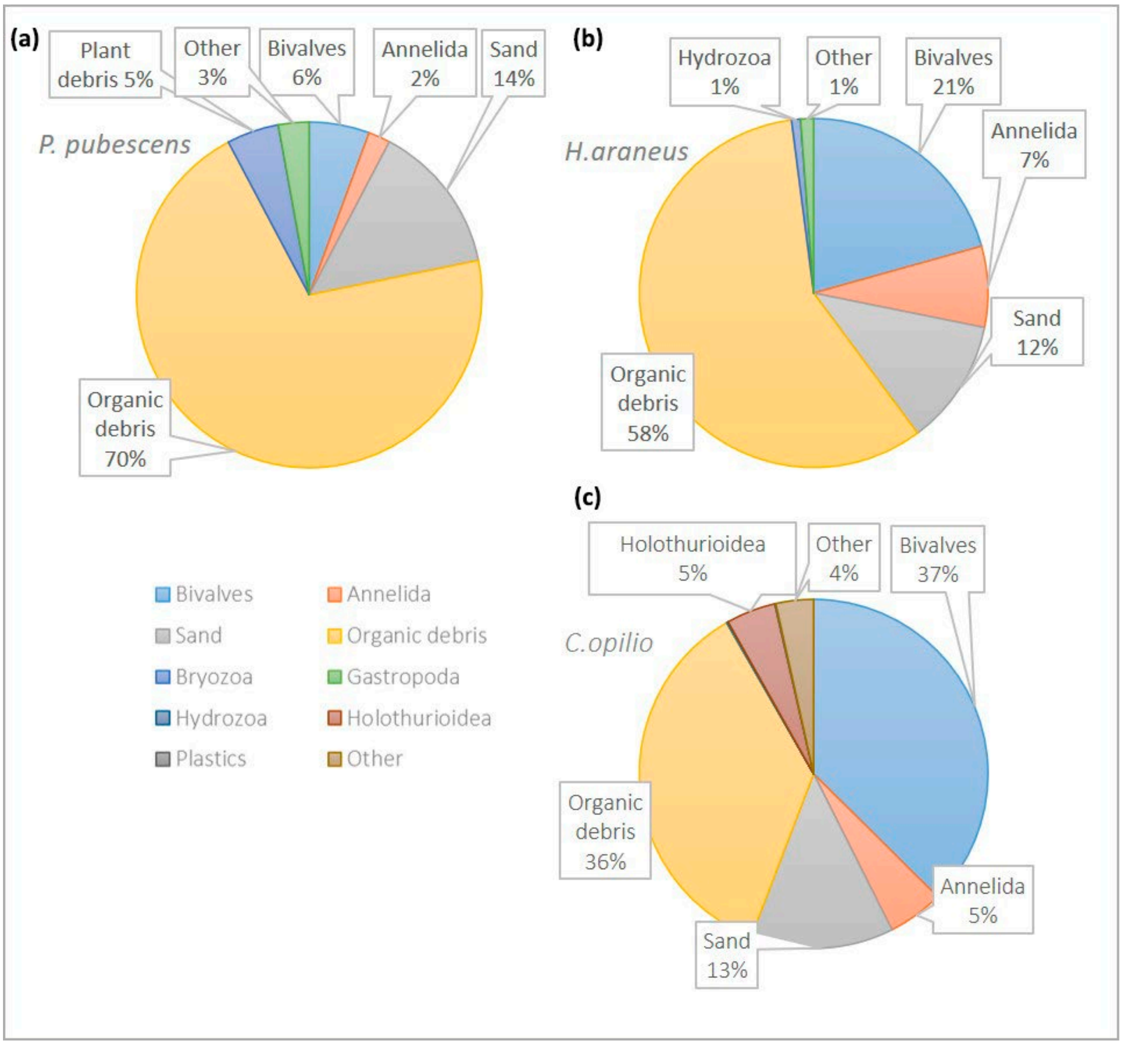

Fig. 3.4 - 4. Food lumps with relative proportions (%) of key prey items to total volume (A) For *P. pubescens*; (B) For *H. araneus* and (C) For *C. opilio*. Figure published in Gebruk et al., 2021b.

Overlap in diets

Neither the UPGMA hierarchical cluster analysis nor the nMDS revealed clear differences in prey item composition between the three species, indicating dietary overlap. However, *P. pubescens* tended to separate more from *C. opilio* and *H. araneus* than *C. opilio* and *H. araneus* between each other (Figure 3.4-5).

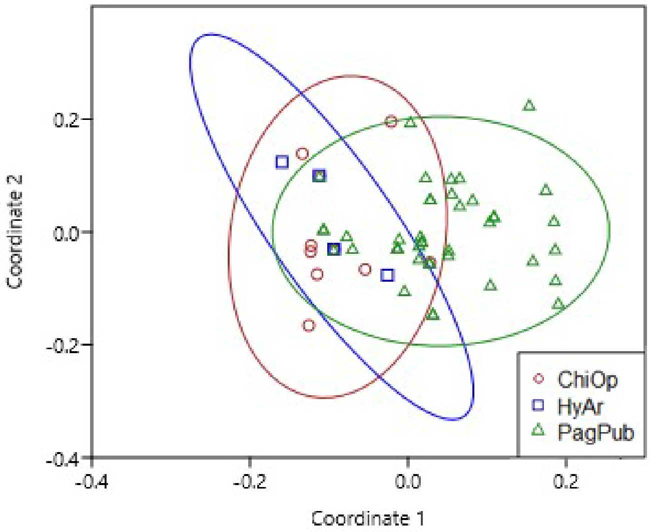

Fig. 3.4 - 5. Stomachs of different species grouped by the nMDS (95% ellipses), calculated with Bray-Curtis similarity measure. Stomach of *C. opilio* shown with red circles; *H. araneus* – blue squares, *P. pubescens* – green triangles. Figure published in Gebruk et al., 2021b.

For all pairs of species, Pianka's measure (calculated for frequencies of occurrence of prey items) was close to 1.0, representing almost full overlap in feeding resources. However, overlap between *C. opilio* - *H. araneus* (0.97) was higher than between *P. pubescens* and brachyuran crabs (0.75 for *C. opilio* - *P. pubescens* and 0.77 *H. araneus* - *P. pubescens*). Pairwise comparison of diets of the three species using ANOSIM and Bray-Curtis similarity measure both agreed with Pianka's index suggesting close proximity between diets of *C. opilio* and *H. araneus* (0.67 similarity measure and no significant difference ($p>0.05$) according to ANOSIM). However, they disagreed with the overlap measure in assessing relationship between *P. pubescens* and other decapods: Bray-Curtis and ANOSIM showed low similarity and significant difference between *P. pubescens* and larger decapods (Table 3.4-2). Overall prey item compositions of *C. opilio* and *H. araneus* diets were close to each other, whilst stomach contents of *P. pubescens* were slightly different from both other species.

Table. 3.4 - 2. Pairwise comparison of diets of three species with Pianka's niches overlap measure; Bray-Curtis similarity measure and ANOSIM analysis ($p<0.05$ showed with green shading). Table published in Gebruk et al., 2021b.

	Index value
Pianka's niches overlap index	
C. opilio - H. araneus	0.97
C. opilio - P. pubescens	0.75
H. araneus - P. pubescens	0.77
Bray-Curtis similarity measure	
C. opilio - H. araneus	0.67
C. opilio - P. pubescens	0.27
H. araneus - P. pubescens	0.39
ANOSIM (significance of difference based on Bray-Curtis similarity index)	
C. opilio - H. araneus	p=0.39; R=0.01
C. opilio - P. pubescens	p=0.001; R=0.81
H. araneus - P. pubescens	p=0.004; R=0.46

Species accumulation curves

Species accumulation curves were used to assess cumulative number of prey items in diets of the three species. The most diverse diet was in *P. pubescens*, comprising all 19 categories of discovered items, followed by *C. opilio* (16 categories) and *H. araneus* (11 categories). However, species accumulation curves showed that in fact snow crabs acquired diet components faster than two other species, with predicted increase in the number of stomachs increasing the number of prey items. This was confirmed by the Chao-2 estimator calculated for predicted total number of prey items. The expected values were: 33 for *C. opilio*, 18 for *H. araneus* and 27 for *P. pubescens.* Conversely, accumulation curves for hermit crabs were close to reaching a plateau for the given number of stomachs (Figure 3.4-6). Observed tendencies and estimation of total number of prey items both confirm the wider trophic niche of newcomer *C. opilio* in comparison with native species.

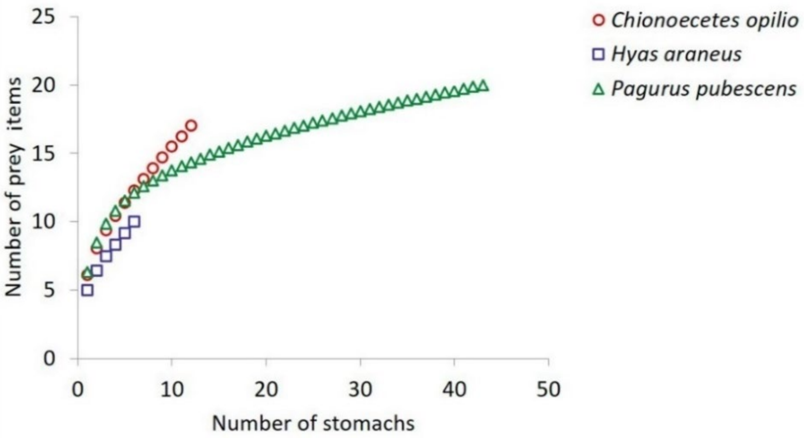

Fig. 3.4 - 6. Species accumulation curves of *C. opilio* shown with red circles; *H. araneus* – blue squares, *P. pubescens* – green triangles. Figure published in Gebruk et al., 2021b.

To summarise, the analyses of stomach contents of *C. opilio*, *H. araneus* and *P. pubescens*, showed that the diets of the three species substantially overlap with *C. opilio* accumulating prey items faster than the native decapod species.

3.5. Discussion

3.5.1. Distribution and population dynamics of *C. opilio* in the Pechora Sea

The ROV video footage obtained in the present study showed presence of *C. opilio* population in the Pechora Sea. According to the latest report by PPINRO (Bakanev and Pavlov, 2020) *C. opilio* is widespread in the Barents Sea with the most successful fishery operations in the north-eastern part of the Barents Sea, from the west shores of Novaya Zemlya islands to Frantz Josef Land (Figure 3.5-1). Notably, only a few data points are available for the Pechora Sea from the ecosystem monitoring programme (Bakanev and Pavlov, 2020).

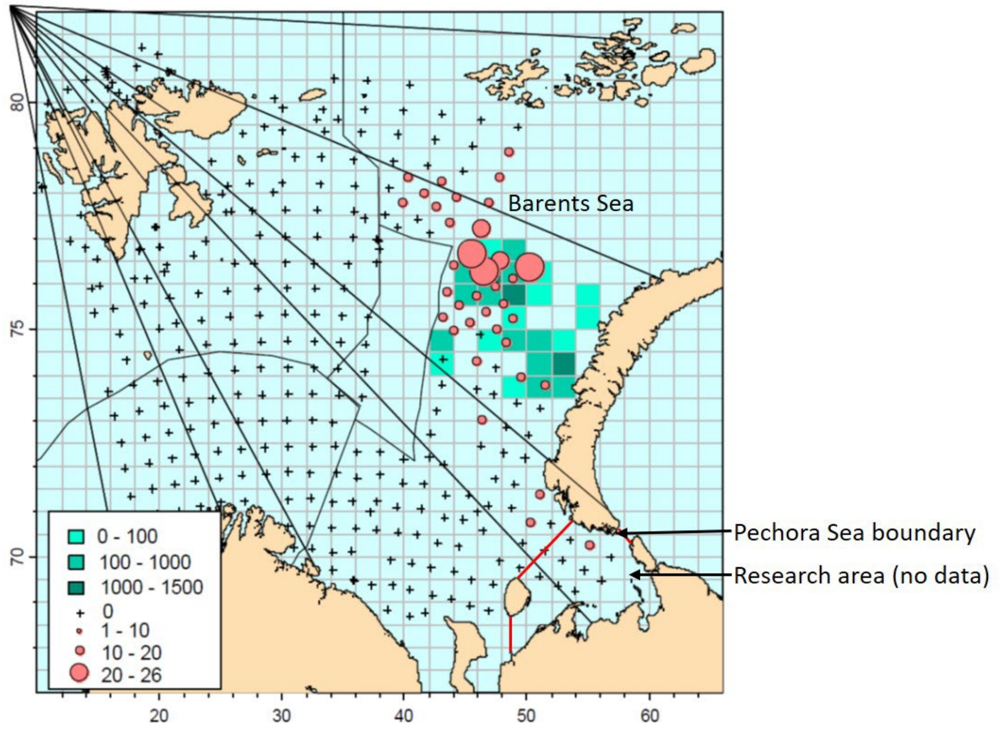

Fig. 3.5 - 1. *C. opilio* fishery in the Barents Sea LME in 2019: green rectangles represent commercial fishery efforts (tonnes per grid), and red circles represent ecosystem monitoring (kg/trawl). Figure adapted from Bakanev and Pavlov, 2020.

Assuming that video footage was comparable across years, despite visibility and current differences, no significant differences in both *C. opilio* occurrence in video recordings and proportion of all decapods were found. Larger data sets, better resolution, more even lighting and close control of environmental variables may help statistically verify the hypothesis of the increased *C. opilio* density in the research area. It is therefore crucially important to continue observations and improve the data collection protocols to understand the state and dynamics of *C. opilio* population in the Pechora Sea and specifically in the foraging grounds of the Atlantic walruses.

The recent study of *C. opilio* invasion in the Kara Sea suggests combining data from scientific trawling and video recording to adequately assess population structure (Zalota et al., 2019). It has been shown that large crabs can escape bottom trawls used in environmental monitoring, therefore there is likely a bias towards juvenile groups in trawling surveys (Zalota et al., 2018) whereas ROV surveys equipped with laser pointers allow to assess size composition but lack other valuable details such as sex ratio (Zalota et al., 2019).

C. opilio reach functional maturity after the terminal moult which typically occurs at CL ranging from 60–120 mm (Conan and Comeau, 1986), however in the Kara Sea mature females have been reported at smaller size range (30 mm, Zalota, 2017). In the present study all males were identified as juveniles based on the discriminant morphometric function (Conan and Comeau, 1986) (Y=0.733–0.988, mature males at Y>1). All *C. opilio* were below commercially harvested size range (CW 26–42 mm whereas average CW of the commercially harvested species is estimated as 118–120 mm, Bakanev and Pavlov, 2020), which suggests that the Pechora Sea can likely act as nursery grounds for smaller specimens similarly to the Novaya Zemlya bays in the Barents Sea (Zalota et al., 2019).

3.5.2. Trophic niches of the *C. opilio, H. araneus* and *P. pubescens* in the Pechora Sea (published in Gebruk et al., 2021b)

From the analyses of stomach contents of *C. opilio*, *H. araneus* and *P. pubescens*, it is clear that the diets of the three species substantially overlap. This is not surprising considering similar feeding habits and co-occurrence in the same feeding grounds, and that - all three decapods are benthic omnivores foraging on macrobenthic communities. Co-occurrence of the two native Barents Sea species (*H. araneus* and *P. pubescens*) was previously reported during the field observation experiment on scavenging behaviour of *H. araneus* near Spitsbergen (Svalbard) (Markowska et al., 2008). However, during that experiment *P. pubescens* individuals were near the bait (cod) but no scavenging activity was observed, whereas *H. araneus* actively consumed the bait (17 crabs were observed during the experiment) (Markowska et al., 2008). This can be considered as a circumstantial evidence that *H. araneus* and *P. pubescens* do not share a carrion prey.

Prey item composition of stomach contents showed that the diets of all three species consisted of bivalve molluscs and polychaetes with minor contribution from other taxa, in this area at the study time. Noticeably, most frequent bivalve fragments in the stomachs (*C. ciliatum*, *E. tenuis*, *M. calcarea* and other) did not exactly correspond to the list of dominant macrobenthic species known for the area (*A. borealis*, *A. montagui*, *M. calcarea*, *S. groenlandicus*, *C. ciliatum*) (Chapter 2; Gebruk et al., 2021a). This could be the result of limitations in taxonomical resolution of visual identification for stomach contents. Only fragments with preserved identifying features (usually hard structures) could be identified to species level, whereas larger items including most of the bivalve species appeared as non-identifiable fragments, generally referred to as bivalve shells.

The morphological analysis revealed that smaller prey items (including foraminifers, hydrozoans, ostracods, nematodes, and others) played an important role in the diet of *P. pubescens*, whereas they were absent or scarce in diets of *C. opilio* and *H. araneus* (Figure 3.4-4; Figure 3.4-5). I suggest that the size of predators and the size of prey items are key factors determining diets of the three decapods (prey-size selectivity has been described for other decapod species including stone crab *Menippe mercenaria* (Say, 1818) and blue crab *Callinectes sapidus* Rathbun, 1896 (Wong et al., 2010)). Larger items including bivalve molluscs *A. borealis*, *S. groenlandicus* and *C. ciliatum* are available for larger snow crabs and great spider crabs, whilst smaller hermit crabs utilize more diverse but smaller infauna. The pairwise comparison of prey item composition of the three species using Pianka's overlap measure, Bray-Curtis similarity measure and ANOSIM test showed an overlap between the three species with stronger affinity of *C. opilio* and *H. araneus* diets, and slightly different stomach content in *P. pubescens*. Differences in diets are mainly attributed to the size of prey items as well as differences in claw morphology between Anomura (*P. pubescens*) and Brachyura (*C. opilio* and *H. araneus*). However, for *C. opilio* scooping sand was previously observed by Cunningham (1969) during periods when no larger food was immediately available. Logvinovich (1945) referred to the frequent presence of sediment in the stomachs and intestines of crabs. Foraminifera, minute molluscs and amphipods found in stomach contents probably result from feeding by sieving, as these either burrow in or occur on sediments (Logvinovich, 1945).

Literature on the feeding of *C. opilio* also indicates frequent differences in diets of males and females, although this mostly refers to adult crabs (Wieczorek and Hooper, 1995; Zakharov et al., 2018). The Pechora Sea however is predominantly populated by subadult males and females which do not seem to differentiate in diets to the same degree (Bakanev et al., 2017) perhaps explaining why no sex-related differences were identified in diets of *C. opilio*.

Observations of the food lumps revealed a notable contribution of plant debris to diet compared to other species. This agrees with previous studies, e.g., Zmudczyńska-Skarbek et al. (2015) demonstrated that *P. pubescens* can consume plant material of terrestrial origin in the areas of abundant ornithogenic coastal vegetation in Spitsbergen. Results of this study show that even in the Pechora Sea, where aquatic vegetation is not abundant (Kucheruk et al., 2003) the diet of *P. pubescens* included a substantial proportion of plant debris.

3.5.3. Conceptual diagram of trophic interspecies relationship between benthic predators and macrobenthic communities in the Pechora Sea

Literature sources combined with the outcomes of the present study allow to reconstruct the conceptual diagram of trophic interspecies relationship between benthic predators and macrobenthic communities in the Pechora Sea (Figure 3.5-2).

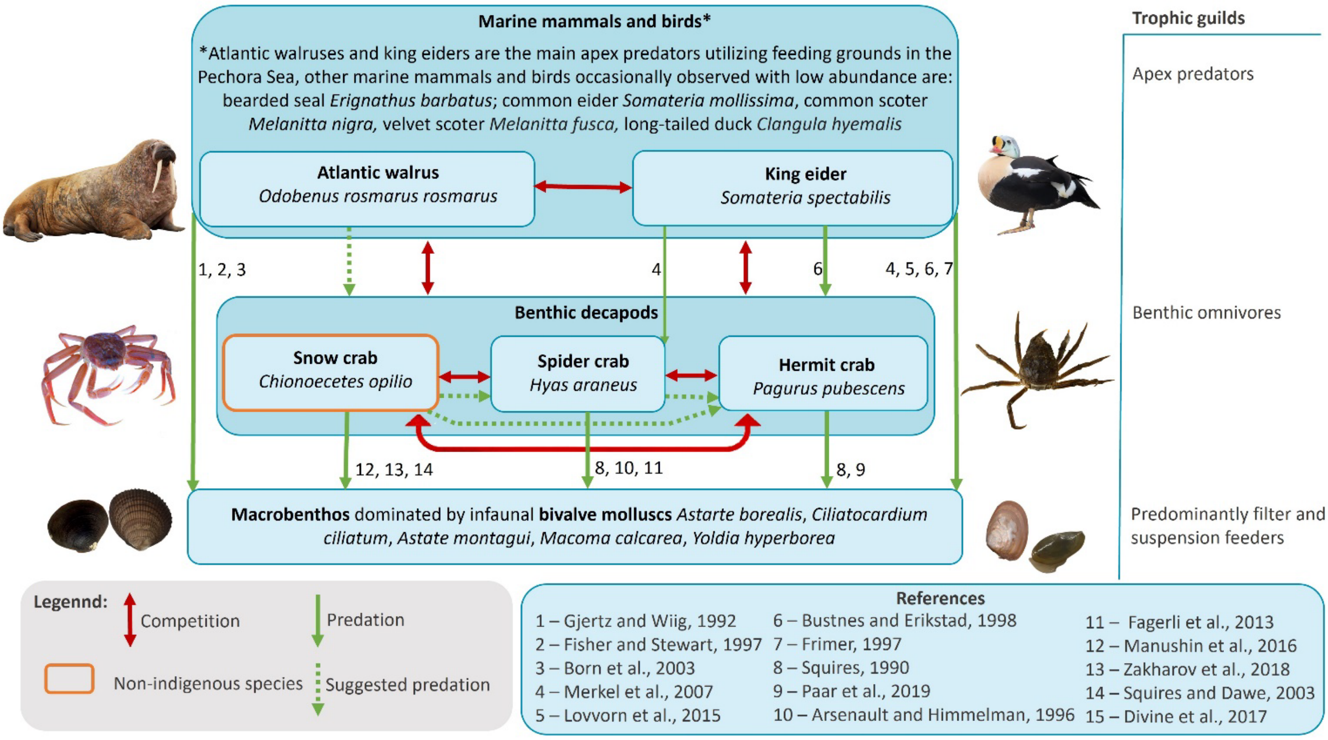

Fig. 3.5 - 2. Conceptual diagram of trophic interspecies relationship between benthic predators and macrobenthic communities in the Pechora Sea.

The diagram demonstrates three key trophic levels: (1) apex benthic predators, predominantly occupied by Atlantic walrus and King eider (other apex predators that are sometimes registered in the region but with low abundance include the following species - bearded seal *Erignathus barbatus*; common eider *S. mollissima*, common scoter *M. nigra,* velvet scoter *M. fusca,* long-tailed duck *Clangula hyemalis*; (2) mobile benthic omnivores, represented by decapods *C. opilio* (NIS), *H. araneus* and *P. pubescens*; (3) macrobenthos dominated by infaunal bivalve molluscs *A. borealis*, *C. ciliatum*, *A. montagui*, *M. calcarea*, *Y. hyperborea*. Numerous scientific publications describe predation of walruses (Gjertz and Wiig, 1992; Fisher and Steward, 1997; Born et al., 2003; and other) and King eiders (Bustnes and Eriksad, 1998; Merkel et al., 2007; Lovvorn et al., 2015; and other) on macrobenthos. The bulk of their diets is formed of bivalves, although most of the trophic studies in the Arctic region also mention other groups of invertebrates, including crustaceans. However, there is currently little evidence of predation of Atlantic walruses or King eiders specifically on *C. opilio*, *H. araneus*, or *P. pubescens* (one study of gullet contents of King eiders in Greenland reports *H. araneus* amongst dominant species in their diets, Merkel et al., 2007). The unresolved questions include whether Atlantic walruses in the Pechora Sea can forage on decapods and specifically on *C. opilio*, and whether *C. opilio* can feed on smaller decapods including hermit crabs and juvenile spider crabs. For the Pacific walrus (*Odobensus rosmarus divergens*) there are reports of predation on decapods (Sheffield and Grebmeir, 2009) including *Chionoecetes*, *Hyas* and *Pagurus* (Fay et al., 1984). It therefore seems possible that Atlantic walruses can utilise *C. opilio* population as an additional foraging resource, and targeted studies for the traces of DNA from *C. opilio* in walruses' faecal pellets can provide sufficient evidence to resolve this question.

3.5.4. Limitations of the methodological approach of this study

Limitations of imagery data interpretation

ROV video recordings can provide valuable georeferenced imagery data, and video surveys are becoming an increasingly popular complementary non-destructive method of benthic assessments (López-Garrido et al., 2020). However, there are several limitations to these data, some of which have been encountered during this study, including the following: (1) visibility of video recording can be severely impacted by local oceanographic conditions, including turbidity, muddy sediments, light conditions, etc; (2) potential bias can be introduced by double-counting of biota; (3) taxonomical identification not always possible, as morphological features are indistinguishable on the footage; (4) assessment of the size structure of populations can be complicated if the size references are missing in the recordings. There are several recommendations that can be adopted to overcome these drawbacks and improve imagery data for quantitative and qualitative assessment:

1. To provide a size reference for estimating size of organisms (objects) and distance

from the floor, it is recommended to use parallel laser pointers spaced at the known distance apart (De Clippele et al., 2017).

2. Where possible it is recommended to position the frontal surface of cameras in parallel to the seafloor, and keep consistent speed, direction and distance from the seafloor to achieve quantifiable linear transects (Mokievsky, 2019). More even lighting is also recommended and can be achieved with a use of light diffusers.
3. Close control of environmental variables (e.g., currents).
4. Sufficient size data sets are needed to enable the use of models. For example, for species distribution models it was shown that the maximum accuracy is reached at 100 data points (Stockwell and Peterson, 2002).

In general, there is a lack of standardisation in the approaches to ROV seascape video assessments (Mokievsky, 2019) and it is recommended to incorporate harmonised protocols of video assessments into the long-term monitoring of the Pechora Sea benthic ecosystems. To achieve maximum accuracy estimating the population of the snow crab specifically, and assess full scope data for different size groups, it is recommended to combine data from video recordings, trawl sampling and baited pots or traps (Zalota et al., 2019). It was shown in the example of the Kara Sea, that adult crabs are underreported in trawl samples as they can actively escape from the trawl whereas smaller specimens are underreported in video recordings due to burrowing, and therefore best results may be achieved when combining these data sources (Zalota et al., 2019).

Limitations of the morphological analysis in feeding studies

Several morphological studies of stomach content have pointed out limitations of this method. These include low taxonomic resolution and difficulty to assess relative importance of prey items. This is because many prey types remain underreported due to loss of distinctive diagnostic features as a result of digestion (Tarverdieva, 1981; Squires and Dawe, 2003). In addition, integrity of the shell fragments can cause bias towards greater contribution of bivalves in food lumps. This limitation of the present study is further complicated by relatively small (especially for *Hyas araneus*) and temporally restricted samples. Loss of data can also occur from empty stomachs, e.g., in this study 22% of stomachs were excluded from the analyses as empty or near-empty. Combination of morphological analysis with other methods can help to overcome these drawbacks. Specifically, combination of morphological analysis of stomach contents with stable isotope analysis allowed to verify the overlap of trophic niche of *C. opilio* with *H. araneus* and *P.*

pubescens. Additional methods are required to explain specific interspecies relationships. As such, to resolve trophic relationship between the Atlantic walrus and the snow crab in the Pechora Sea, it is recommended to use molecular genetic methods to trace *C. opilio* DNA in walrus faecal samples.

The composition of stable isotopes of carbon and nitrogen in animal tissues is used in feeding ecology as an emergent property of dietary niches and habitat use (Post et al., 2007; Flaherty and Ben-David, 2010). This is because carbon/nitrogen ratios in the tissues of aquatic organisms provide information on the source of feeding ($\delta^{13}C$) and relative trophic position ($\delta^{15}N$) (Linnebjerg et al., 2016; Odintsov and Kiyashko, 2018). The term “isotopic niche” (Newsome et al., 2007) is broadly used in stable isotope analyses. It is defined as an area in $\delta^{13}C/\delta^{15}N$ space that characterises the trophic resources and habitat use of the species. Comparison of an overlap in dietary niches determined by stomach content analyses with overlap in isotopic niches based on stable isotope analysis could allow to gain a better understanding of the trophic relationships between the three benthic decapod species in the Pechora Sea.

Stable isotope analysis of 40 decapod specimens was conducted by Anna Zalota, IO RAS to compare with the outcomes of this study, isotopic niche parameters were calculated using the Stable Isotope Bayesian Ellipses, full methods described in Gebruk et al. (2021b). Overall, stable isotope analysis showed a clear discrepancy of isotopic niches between *H. araneus* and *P. pubescens*, provided that within one sampling site niches overlapped less than among all samples. The isotopic niches of *C. opilio* overlapped with both native decapod species to a greater extent. The lowest overlap was between *H. araneus* and *P. pubescens* without area differentiation (Gebruk et al., 2021b). Overall, *C. opilio* had overlapping stomach contents composition and overlapping isotopic niche with both native decapod species, however, to understand the extent to which the new competitor may alter the future biodiversity of Pechora Sea, long term studies of biodiversity are now needed.

3.6. Recommendations for ecological monitoring

This study showed presence of the *C. opilio* in the foraging grounds of Atlantic walruses near Vaigach Island and overlapping dietary niches of *C. opilio* with native benthic decapods *H. araneus* and *P. pubescens.* However, to better understand the population dynamics of the snow crab in the Pechora Sea and extent to which the new competitor may alter the future benthic biodiversity of Pechora Sea, long term studies of biodiversity are now needed. It is recommended to combine data from different sources to increase spatiotemporal resolution of future studies.

Specific recommendations on the methods required to resolve trophic interspecies relationships of the snow crab with other benthic predators and state of the snow crab population in the Pechora Sea include the following:

Combination of data from **multiple sources** needed to assure complex assessment of benthic ecosystems including mobile megafauna.

- Combination of scientific trawls, baited traps and ROV assessments is recommended to assess full scope data for different size groups.
- ROV video observations are recommended for assessment of mobile megafauna in the Pechora Sea. Parallel laser pointers spaced at a known angle and distance apart (laser scale) are recommended to provide size reference. Keeping the speed, direction, lighting and distance from seafloor consistent can improve the quality (and quantity) of data.
- To resolve trophic relationship between the snow crab and the Atlantic walrus, molecular genetic analyses is needed to trace the crab DNA in walrus faecal samples.

3.7. Summary

The snow crab *Chionoecetes opilio* is the only NIS reported in benthic ecosystems of the Pechora Sea in the Arctic Biodiversity Assessment (CAFF, 2013) and more recent scientific literature. However, since the Pechora Sea lies outside of the commercially harvested range of *C. opilio*, little is known about its regional state of population, trophic interactions with other benthic predators and long-term ecosystem consequences of introduction.

Analysis of ROV video footage from the feeding grounds of Atlantic walruses near Vaigach Island showed presence of *C. opilio* in 2016 and 2020. However larger data sets are needed to better understand population dynamics of the snow crab in the area. The relatively small carapace size of study *C. opilio* (no males had reached maturity according to the discriminant morphometric function) suggest that the Pechora Sea could have a role of nursery grounds similarly to those in the nearby fjords of Novaya Zemlya (Zalota et al., 2019).

Stomach content analysis demonstrated overlap in the diets of *C. opilio*, the spider crab *Hyas araneus* and the hermit crab *Pagurus pubescens*. If these resources are limiting this suggests that the snow crab may be competing for food with native decapods. Diets of *H. araneus* and *P. pubescens* overlapped to a lesser extent, due to differences in claw morphology and prey sizes. All three species were feeding on macrobenthos and had nonspecific diets comprising a total of 20 prey item categories.

Conceptual diagram of trophic interspecies relationship between benthic predators and macrobenthic communities in the Pechora Sea was developed (Figure 3.5-2). The present study demonstrates direct trophic competition between *C. opilio* and native benthic decapods, however the trophic relationship between the Atlantic walrus and *C. opilio* remains uncertain. Long-term observations of benthic biodiversity, and populations of *C. opilio* and the Atlantic walruses are needed to understand impacts of the invader on the future biodiversity and ecosystem functioning of the Pechora Sea.

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Chapter 4. Spatial and temporal variability of plastic ingestion by benthic invertebrates in the Eurasian Arctic

Chapter focus

Chapter 4 investigates the accumulation of microplastics in the benthic ecosystem of the Eurasian Arctic. Three groups of samples of macrobenthos were studied for microplastic ingestion: (1) field samples collected from the Pechora Sea in 2017–2018 to assess the baseline level of microplastic ingestion in the Pechora Sea; (2) historic samples from zoological collections of the Shirshov Institute of Oceanology collected from the Pechora Sea in 2008 to assess temporal change in accumulation of microplastics; (3) field samples collected from the Kara Sea, Laptev Sea and East-Siberian Sea in 2019 to compare microplastic pollution the Pechora Sea with other regions of the Arctic. A conceptual diagram of accumulation of microplastics in benthic ecosystem of the Pechora Sea was presented and discussed. The chapter begins with a literature review of the state of knowledge on the effects of microplastics on marine biota and distribution of microplastics in Worlds Ocean.

4.1. Abstract

Microplastics in the ocean have been declared an emerging threat to ocean health and status under the United Nations Sustainable Development Goal 14. Yet our knowledge on distribution and accumulation of microplastics in the Arctic Ocean remains scarce. Accumulation of microplastics in benthic fauna is of particular concern as it can build up in commercially important species through the food web. A baseline assessment of microplastic ingestion by Arctic benthic fauna is of urgent necessity, and no data were available for the Pechora Sea prior to this study. The goal of this chapter was to provide baseline data on ingestion of microplastics by benthic fauna in the Eurasian Arctic.

To assess spatial and temporal variability of microplastic ingestion by benthic invertebrates, stomach contents were examined for the presence of microplastics with a combination of dissection and digestion methods. A collection of 211 benthic invertebrates sampled in the Pechora Sea in 2017–2018 were studied, and an additional 73 specimens were collected in the Pechora Sea in 2008. Finally, 49 specimens were sampled from other regions of the Eurasian Arctic, namely the Kara, the Laptev and the East-Siberian Seas in 2019.

Bivalve molluscs and decapod crustaceans were the most abundant groups of benthic invertebrates, representing feeding modes of suspension feeders, deposit feeders and mobile benthic omnivores. Variation of microplastic ingestion across the feeding guilds, species, years, and regions was assessed with a combination of statistical tests including ANOSIM, nMDS, UPGMA hierarchical cluster analyses, non-parametrical Kruskal-Wallis test, the Clopper-Pearson multiple proportion intervals, Chi-squared test. Microplastic fibres were recorded in 29% of all samples of the Pechora Sea macrobenthos. No relationships were found between the occurrence of microplastic and size/weight of animals. No significant differences in the occurrence of microplastic were identified between the species, feeding guilds or sampling sites. Noticeably lower average frequency of ingested microplastics was recorded for the historical samples from 2008 (9%) than in the field samples collected in 2017–2018. Differences in microplastic accumulation in 2008 and 2017–2018 were proven statistically significant with an ANOSIM test (R=0.46; p=0.008), and a Chi-squared test (p=0.0006; RD=-0.19; Chi-2=10.08). SIMPER analyses revealed an overall average dissimilarity 71.11% between the years with the greatest contributions to dissimilarity from *A. borealis* (61%) and *M. calcarea* (28%). Similar occurrences of microplastic were estimated in all studied regions of the Eurasian Arctic (average 27±2%) with lowest value in the East Siberian Sea (25%) and highest in the Pechora Sea and the Laptev Sea (29%).

A harmonised monitoring program is needed for monitoring of microplastic pollution in the Arctic with consideration of regionally specific features, such as seasonality of the ice cover, primary production and riverine discharge. Recommendations for further microplastics studies include adding occurrence of microplastic in benthic fauna to the SDG 14 as a globally important indicator of plastic pollution and comprehensive monitoring of microplastic ingestion by commercial species of invertebrates (the red king crab *Paralithodes camtschaticus*, the snow crab *Chionoecetes opilio* and the Iceland scallop *Chlamys islandica* O. F. Müller, 1776) in the Barents Sea).

4.2. Introduction

4.2.1. Introduction to marine microplastics and effects on marine biota

Plastic litter and microplastics in marine ecosystems: types and sources

Plastic litter in the marine environment has been reported globally as the most abundant form of marine debris. Up to 80% of the world's marine litter corresponds to plastics according to United Nations Environmental Programme surveys (UNEP, 2016). Up to 10% of global plastic production estimated to enter the oceans annually (Avio et al., 2017), and may cause adverse impacts ranging from direct impacts on marine biota and habitats causing mortality and transporting non-indigenous species, to aesthetic impacts of litter leading to loss of tourism and economic damage (Avio et al., 2017). Lack of knowledge regarding the extent of plastic pollution in the Arctic Ocean, one of the world's most sensitive areas to environmental change, makes baseline research of critical importance.

Plastics are synthetic polymers with thermo-plastic or thermo-set (non-deformable) properties (Kershaw et al., 2019). The most common types of plastics in the marine environment include high-density and low-density polyethylene (LDPE and HDPE), polypropylene (PP), polyethylene terephthalate (PET), polyvinylchloride (PVC), polystyrene (PS), polyamide (PA) and nylon cellulose acetate (CA) (Wright et al., 2013; Avio et al., 2017; Kershaw et al., 2019). Plastic polymers have different densities, which determines their environmental "fate" and behaviour assuring whether particle will float in the surface, stay in the water column, or sink to the seafloor (Avio et al., 2017). PE, PP and PS have lower densities than seawater, making them the most commonly occurring floating plastics; whereas PET, PA and PVC are denser than water and are common in the bottom sediments (Wright et al., 2013; Kershaw et al., 2019). Although most plastic polymers are chemically inert, production of plastics involves additives including flame-retardants, UV stabilisers, antioxidants, plasticisers, stabilisers, fillers, pigments and lubricants that can pose biological hazards when ingested (Avio et al., 2017; Barrows et al., 2018; Kershaw et al., 2019).

Plastic production increased dramatically worldwide since the beginning of large-scale plastic manufacturing in the 1950s and reached 368 million tonnes in 2019 (Plastics Europe, 2020). Key sources of plastics in the oceans include terrestrial inputs from riverine continental run-off, wastewater discharge, wind and tidal transport of coastal litter; and offshore including litter and gear from maritime activities and long-range transport from other ocean basins (Cooper and Corcoran, 2010; Avio et al., 2017; Barrows et al., 2018). Majority of plastic items globally are produced by packaging industry (36%), followed by building and construction (16%) and textiles (15%) (Kershaw et al., 2019), in the oceans these ratios may vary but textile microfibres are often find as the most abundant form of litter (Lusher et al., 2015). After entering the marine environment, plastic items degrade into smaller particles that become bioavailable for a wide range of marine organisms as a result of mechanical fragmentation, partial biodegradation and photodegradation (Singh and Sharma, 2008; Reisser et al., 2014; Rochman et al., 2014). Microplastics are defined as plastic particles of 1 µm – 5 mm diameter for globules or length for fibres (Arthur et al., 2008). Marine microplastics consist of primary microplastics – particles manufactured <5 mm in diameter (powders, resin pellets, microbeads from cosmetics and cleaning products, fibres from clothes) and secondary microplastics, resulting from the degradation of larger plastic items (bags, bottles, packaging, fishing nets and other) (La Beur et al., 2019). Nanoplastics are particles <1 µm that are not routinely considered for environmental monitoring due to technical difficulties with quantifying and identifying their chemical structures (Kershaw et al., 2019); thus, little is known about concentrations and impacts of nanoplastics in the marine environment.

Interactions of marine organisms with plastic debris

The growing presence of plastic items in the marine environment leads to increasing magnitude of exposure of marine biota to plastics, with a range of physiological, biochemical and ecological consequences ranging from transportation of non-native species to blockages of digestive systems (Azzarello and Van Vleet, 1987; Laist, 1987; Quayle, 1992; Derraik, 2002; Gregory, 2009; Teuten et al., 2009; Zettler et al., 2013; Lusher et al., 2013; Avio et al., 2017). Most of the interactions of marine biota with plastics documented in literature have impacts at the organism- or suborganism level, such as entanglement or ingestion, but it has been predicted that impacts from beyond the population level, such as impacts on assemblages, habitats and ecosystems, are the most ecologically relevant (PAME, 2019). It has been also predicted that plastic pollution can have a combined effect with other anthropogenic stressors, where it is difficult to quantify ecological effect of any singular stressor in isolation (PAME, 2019).

Entanglement is a well-recorded example of interaction of marine biota with larger plastic debris such as synthetic ropes, nets, monofilament lines and packaging (Page et al., 2004; Gregory, 2009). Entanglement can lead to lethal injuries or death from starvation, debilitation and demobilisation (Gregory, 2009). Cases of entanglement have been widely recorded for marine mammals including pinnipeds (Fowler et al., 1989; Fowler, 2000; Kiyota and Baba, 2001); cetaceans (Sadove and Morreale, 1989; Neilson et al., 2009); and even polar bears (Bergmann et al., 2017a).

Floating plastic debris can create new habitats for microorganisms, so-called “plastisphere” communities, comprising bacteria, cyanobacteria, diatoms, coccolithophores, ciliates, bryozoans, and others (Zettler et al., 2013; Reisser et al., 2014). Floating plastics can also act as vectors for biological invasions by transportation of non-native species over large distances (Barnes, 2002; Zettler et al., 2013).

Ingestion is the most common interaction of animals with microplastics particularly when feeding mechanisms do not discriminate between plastic particles and food items (Courtene-Jones et al., 2018; La Beur et al., 2019). Presence of microplastics in zooplankton species is of particular ecological concern, since ingestion by organisms from the primary trophic levels (zooplankton) is a pathway for transfer of microplastics into the pelagic food web (Avio et al., 2017), though implications for the Arctic marine ecosystem functioning are yet to be determined. Researchers have not yet determined effects from microplastic ingestion by humans, however, accumulation of microplastics in marine biota and especially commercially valuable species does lead to food security concerns related to transport of environmental pollutants by plastic particles and leaching of toxic additives such as phthalates, bisphenol A (BPA), alkylphenols and others (Hirai et al., 2011; Rochman et al., 2014). Recent World Health Organisation (WHO) assessment of hazards from microplastics in drinking water to human health revealed insufficient information to draw firm conclusions (WHO, 2019). Notably, risks related to accumulation of microplastics in seafood have not been thoroughly assessed yet. Experimental studies on fish and invertebrates showed complex physiological and biochemical responses to exposure to contaminated microparticles including disruption of synthesis of endogenous hormones, down-regulation of DNA processing, onset of oxidative stress, inflammation reactions (Teuten et al., 2009; Von Moos et al., 2012; Browne et al., 2013; Mazurais et al., 2015).

4.2.2. Microplastics in benthic ecosystems

Benthic ecosystems are predicted to constitute a global sink for marine microplastics as a result of direct sinking, biodegradation, biofouling or ingestion and transport of microplastic particles through the food webs (Galgani et al., 1996; Derraik, 2002; Thompson et al., 2004; Bergmann and Klages, 2012; Van Cauwenberghe et al., 2013; Avio et al., 2017; Kane et al., 2020; Mohrig, 2020). Particularly in the deep-sea, complexity of topographic and hydrographic regimes acts to funnel marine litter and microplastics in the seafloor ecosystems (La Beur et al., 2019). Recent study in the Tyrrhenian Sea revealed that thermohaline-driven bottom currents are primarily responsible for distribution of microplastics in the seafloor and can create microplastic hotspots with as much as 1.9 million particles/m^2 (Kane et al., 2020). It has been also predicted that deep-sea biodiversity hotspots are likely linked to the microplastic hotspots since the same thermohaline bottom currents that transport the plastic litter also supply nutrients to benthic fauna enabling formation of hotspots (Kane et al., 2020). Still, there remain very few studies dedicated to microplastics in deep-sea ecosystems, and almost none for the Arctic Ocean apart from a recent study in the HAUSGARTEN Observatory in eastern Fram Strait (Bergmann et al., 2017b).

It is likely that ingestion is the most common form of interaction of macrobenthic invertebrates with microplastics (Avio et al., 2017; La Beur et al., 2019). Ingested microplastics have been identified in macrobenthic organisms in the deep-sea North Atlantic (Courtene-Jones et al., 2018; La Beur et al., 2019), mid-Atlantic and Indian Oceans (Taylor et al., 2016), and in the Ross Sea in Antarctica (Sfriso et al., 2020). Studies focusing specifically on the ingestion of microplastics by benthic fauna in the Arctic are lacking with rare exceptions such as the report looking at blue mussels from Svalbard, which showed 90% occurrence of ingested microplastics (Sundet et al., 2016) and more recent study in the Bering and the Chukchi Seas (Fang et al., 2018). In the Bering and Chukchi Seas, 11 species of macrobenthos (n=413) were examined and all showed microplastic ingestion occurrence between 0.04 and 1.67 items individual^{-1} (Fang et al., 2018). No records were found of microplastics in benthic fauna of the Pechora Sea prior to the date of this study.

Although microplastics have been found in macrobenthos globally, there is still little understanding as to how microplastics are ingested by organisms of the different feeding modes and whether they can accumulate in the digestive systems and other tissues of benthic invertebrates over time. Microplastic translocation from digestive systems to body tissues, e.g., from stomachs to circulatory systems is of a great concern. Translocation of polystyrene microspheres from the gut cavity to haemolymph has been shown in blue mussels *Mytilus edulis*, one of world’s most cultivated aquaculture species (Browne et al., 2008). Seafloor invertebrates demonstrate a great variety of feeding strategies that can be classified based on food sources, diet type and feeding mode. Trophic classification of benthic fauna varies but most common feeding guilds usually include suspension feeders (feed on suspended particles in the water), filter feeders (suspension feeders that actively strain suspended particles from water), deposit feeders (collect feeding items from the sediments), grazers (feed by scraping biofilms, algae or epifauna), predators (feed on prey that is live), scavengers (carrion prey), omnivores (non-selective eaters combining different preys), lignivorous (feeding on wood), chemosynthetic (usually feeding through symbiosis with bacteria), parasites (depending on host in getting foraging resources) (Cusson and Bourget, 2005; Arapov et al., 2010; Macdonald et al., 2010). Some species have selective diets and narrow trophic niches whereas others are more flexible, some even show ability to switch between feeding modes depending on food availability. For example, the common boreal bivalve mollusc *Limecola balthica* can adjust the position of its siphon and either have it vertically in the water column to filter suspended particles from water or place it on the surface of the sediment to search for prey items like a deposit feeder (Rasmussen, 1973). Great variability of feeding modes can also be demonstrated by closely related species, e.g., within the *Macoma* genus there are eight species of which some are deposit feeders, some are suspension feeders, some are biofilm grazers, and some can switch between deposit- and suspension feeding strategies (Reid and Reid, 1969). In the Pechora Sea, macrobenthic communities are mostly dominated by the suspension-feeding bivalve molluscs that rely on organic matter from the surface waters.

Some researchers have shown differences in microplastic ingestion between the feeding guilds, whereas other argue that occurrence may vary interspecifically but not between the feeding modes, in general no agreement on which groups are most susceptible to microplastics has been reached (Taylor et al., 2016; Courtene-Jones et al., 2018; La Beur et al., 2019; Sfriso et al., 2020). Differences in microplastic ingestion between the feeding modes had been shown for intertidal species (Setälä et al., 2016); but limited deep-sea studies seem to agree that taxa specific differences prevail over the feeding guild differences (Courtene-Jones et al., 2018; La Beur et al., 2019; Sfriso et al., 2020). One assumption is that mobile benthic predators, and omnivores such as benthic decapods likely consume microplastics passively with their prey or from sediments which could result in higher occurrence due to bioaccumulation (Taylor et al., 2016). In the deep-sea north Atlantic the predatory sea star *Hymenaster pellucidus* Thomson, 1873 contained the highest median number of microplastics than any other species (Courtene-Jones et al., 2018). In contrast, a recent study in Antarctica has shown little evidence of plastic accumulation in food webs with bivalves and gastropods having the highest occurrence among any groups (Sfriso et al., 2020). Non-selective filter feeders may be particularly susceptible to digestion of microplastics as they concentrate prey items from large volumes of water (Sfriso et al., 2020), and these species can include some species of ecosystem-engineering cold-water corals and sponges that construct habitats and provide crucial ecosystem services in deep-water ecosystems (La Beur et al., 2019).

4.2.3. Distribution of plastic debris in the Arctic Ocean

Until recently the Arctic Ocean was considered free of plastic pollution, but this changed significantly in the last years with microplastics have been found in the Arctic waters, sea ice, sediments, and biota (Obbard et al., 2014; Lusher et al., 2015; Bergmann et al., 2017b; Cozar et al., 2017; Fang et al., 2018; Kanhai et al., 2020). Large-scale ocean circulation together with spreading and mixing of river discharge and transportation and release by ice drift are likely the main mechanisms governing distribution of microplastics in the Arctic Ocean (Lusher et al., 2015; Cozar et al., 2017; Yakushev et al., 2021). However, the relative significance of these sources and areas of accumulation of microplastics in the Arctic Ocean remain unknown. Globally floating plastic debris accumulates in the convergence zones, regarded colloquially as “plastic gyres” or “garbage patches”. Five subtropical plastic gyres have been identified in the Pacific, Atlantic and Indian Oceans (Eriksen et al., 2014). The main factors leading to formation of the plastic gyres are stable convergence areas commonly associated with ocean gyres, Ekman transport and the density of human population in upstream coastal regions (Van Sebille et al., 2012; Eriksen et al., 2014). Whilst data on plastic pollution in the Arctic Ocean are scarcer than for other regions, Cozar et al. (2017) reported substantial accumulation of microplastics near the Novaya Zemlya archipelago in the eastern Barents Sea, with concentrations of hundreds of thousands of pieces of debris per square kilometre. Buoyant plastics sourced primarily from eastern seaboard of the US and northwest European shelf are transported by the North Atlantic drift to the Greenland and Barents Seas. Large-scale oceanographic circulation and sinking of water masses make this region likely to accumulate transported plastics from distal sources in the water column and benthic environment (Cozar et al., 2017). This is supported by modelling of surface ocean circulation, which predicts that a sixth garbage patch of floating plastics could accumulate in the Arctic’s Barents Sea over the next few decades (Van Sebille et al., 2012).

With rivers serving as key vectors for terrestrial plastic run-off (Lebreton et al., 2017; Barrows et al., 2018; Hurley et al., 2018), it is also important to consider these as inputs to Arctic marine ecosystems. Continental run-off is a major source of freshwater, nutrients and terrigenous material in the Arctic. The Arctic Ocean accounts for 4% of the area and 1% of the volume of the global ocean but receives 11% of the global freshwater discharge (Gordeev et al., 1996; Fichot et al., 2013). Large Arctic rivers, namely, the Northern Dvina, Pechora, Ob, Yenisei, Lena, Indigirka, Kolyma, Yukon and Mackenzie, drain large areas of Europe, Asia and North America (Figure 4.2-1) (Carmack, 2000; Guay et al., 2001). As a result, these rivers are potentially important sources of plastic litter in the Arctic Ocean as many coastal areas, at least for now, still have relatively small human populations and less human activity taking place in the form of shipping and other offshore industries (Cozar et al., 2017). Freshwater discharge to the Arctic Ocean forms buoyant river plumes that cover wide coastal and shelf areas over millions of square kilometres. The majority of this freshwater volume flows into the coastal areas during a short high-discharge period that occurs in Arctic rivers over several months in spring and summer, driven by permafrost thaw, glacial melting and precipitation events linked to seasonally-high atmospheric temperatures, when coastal and shelf areas are ice-free (Peterson et al., 2002). Therefore, microplastics could remain contained within large river plumes, whose dynamics then determine the spreading and accumulation of plastics in the Arctic Ocean.

Fig. 4.2 - 1. Map showing the major Arctic rivers, ocean currents and human populations. Density of human populations in the Arctic coastal areas and near the rivers contributing to annual freshwater discharge to the Arctic Ocean. Orange dots represent settlements with a population of >5000 people north of the Arctic Circle; blue arrows show directions of prevailing surface currents. Map courtesy of the LMSU MRC.

Results of the recent RV *Akademik Mstislav Keldysh* expedition *AMK*-78 to the Russian Arctic in autumn 2019 demonstrated low concentrations of floating plastic particles but their consistent presence in the surface and sub-surface waters of the Kara, Laptev and East-Siberian Seas (Yakushev et al., 2021). Areas of higher concentrations of floating plastics in the Kara and Laptev Seas corresponded to areas of lower surface salinity, strongly suggesting that distribution of surface microplastics in the Eurasian Arctic shelf seas is directly connected to the transport and dissipation of river plumes, and specifically to the discharge of the Great Siberian Rivers - the Ob, Yenisei and Lena Rivers (Yakushev et al., 2021). Surface distribution and chemical characteristics of microplastics obtained from in situ measurements in the Eurasian Arctic revealed two different sources of floating microplastic, namely, inflow from the North Atlantic and discharges from the Great Siberian Rivers (Yakushev et al., 2021). The spatial distribution of the marine and river-borne microplastics is governed by spreading and transformation of the related water masses. In particular, the North Atlantic drift plays key role in surface water plastic contamination in the Barents Sea, but during its transit through the Barents Sea the Atlantic water submerges below the Polar surface water mass in the northern part of the Barents Sea and its circulation does not influence transport of floating microplastics eastward from the Kara Gate strait (Yakushev et al., 2021).

Transport of microplastics and larger plastic items in the sea-ice and its subsequent release during summertime ice melting is another important vector distributing floating plastic litter to Arctic surface waters (Fichot et al., 2013; Obbard et al., 2014; Kanhai et al., 2020). During the ice formation in autumn, microplastics residing in surface waters are incorporated into the sea ice matrix. Microplastics contained in sea ice are then transported and redistributed by ice drift as a result of wind and ocean circulation patterns during the cold season, before being returned to surface waters during seasonal ice melt, potentially hundreds of kilometres from where the ice formed (Peeken et al., 2018).

4.2.4. Governance and monitoring of microplastics

Plastic debris, including microplastics, is now recognised as a threat to ocean health and is listed among other marine stressors including climate change, ocean acidification, habitat destruction, introduction of non-indigenous species, and overfishing (Amaral-Zettler et al., 2015). The legacy of marine plastic pollution has led governments, international organisations, non-governmental organisations and other stakeholders to recognise the need for assessing and monitoring the magnitude, distribution and sources of plastic pollution throughout the global oceans. Marine plastics debris have been listed as an emerging pollutant under Descriptor 10 of the European Marine Strategy Framework Directive (Directive 2008/56/EC). In addition, the Basel Convention on the Control of Transboundary Movements of Hazardous Wastes and Their Disposal has recently adopted Plastic Waste Amendments that will come into force in January 2021 and add plastic polymers including polyethylene, polypropylene, or polyethylene terephthalate to the list of hazardous wastes requiring removal from the oceans (BC-14/12, see PCPWA, 2021). With a view to building common interests with global inclusion, of great interest is decision BC-14/21 on international cooperation and coordination (BC-14/21) that clearly mandates governments and other stakeholders to develop measures to ensure the effective implementation of the plan “Towards a Pollution-Free Planet”. The Plastic Waste Partnership (PWP) was established under the Basel Convention and is currently developing a workplan for the biennium 2020−2021. The UN has also placed microplastics high on its agenda within the framework of the UN Decade of Ocean Science for Sustainable Development, wherein ‘a clean ocean where sources of pollution are identified and removed’ is stated among the key societal outcomes of the Decade (UNDOS, 2020).

The Arctic Council has also recently recognised plastic pollution in the Arctic marine environment as an emerging threat and carried out the first desktop study on marine litter in the Arctic conducted by the Protection of the Arctic Marine Environment (PAME) Working Group in 2019 followed by the development Regional Action Plan on Marine Litter in the Arctic (PAME, 2019; PAME, 2021). The PAME reports identified multiple knowledge gaps in sources of plastic pollution in the Arctic, the drivers and pathways of distribution, interactions with marine fauna, socio-economic impacts (PAME, 2019). Furthermore, there are no harmonised approaches for assessments of physiological impacts and chemical interactions of ingested microplastics despite the growing evidence of plastic consumption by various marine organisms including commercially-harvested species.

4.2.5. Objectives and scope of this chapter

The aim of this chapter was to address the knowledge gap on ingestion of microplastics by benthic organisms in the Arctic Ocean by examining stomach contents of benthic invertebrates from the Pechora Sea for the presence of microplastics and then assessing spatial and temporal variation in microplastic accumulation. This can be divided into the following **research objectives**:

1) To assess variation of microplastic occurrence across species of macrobenthic invertebrates in the Pechora Sea.
2) To assess variation of microplastic occurrence across feeding guilds of macrobenthos in the Pechora Sea.
3) To assess variation of microplastic occurrence in benthic organisms across sampling sites in the Pechora Sea.
4) To assess variation of microplastic occurrence in benthic organisms across regions of the Eurasian Arctic.
5) To compare microplastic ingestion in samples collected in 2008 and a decade later in the Pechora Sea. A prediction was made to reveal an increase in microplastic occurrence in benthic organisms in time due to increased global plastic production.

Based on the literature review interspecific variability in microplastic contamination of macrobenthos was predicted with suspension-feeding bivalve molluscs likely showing the highest occurrence of microplastics as shown for the other regions (Taylor et al., 2016; Courtene-Jones et al., 2018; La Beur et al., 2019; Sfriso et al., 2020). No previous studies have investigated temporal variability of microplastic contamination of the seafloor fauna. However, based on the increasing rates of plastic production world-wide (Plastics Europe, 2020), higher contamination in 2018 can be expected compared to 2008. Considering the growing evidence of ingested microplastics by benthic organisms globally and in the Arctic, including in the Barents Sea (Halsband and Herzke, 2019), and in the Bering and the Chukchi Seas (Fang et al., 2018), I also expect to find ingested microplastics in the remote areas of the Eurasian Arctic shelf seas that have been never previously assessed for ingested microplastics such as the Laptev and East-Siberian Sea, however it is difficult to predict whether contamination occurrence will be significantly different from the Pechora Sea.

Three groups of samples were obtained and studied as a part of this study:

1) Field samples of macrobenthos collected by author in 2017–2018 in the Pechora Sea were examined to characterise the level of microplastic contamination in the Pechora Sea and establish the first baseline on microplastic contamination for this region (outcomes accepted for publication as Gebruk et al., in press – see Thesis Overview for more detail).
2) Historic samples from the Pechora Sea collected in 2008 and archived by the Shirshov Institute of Oceanology of the Russian Academy of Sciences (IO RAS) were studied to assess temporal variability in occurrence of microplastics.
3) Field samples were collected from the Kara, East-Siberian and Laptev Seas during the RV *AMK*-78 expedition in 2019 to assess spatial variability of microplastic ingestion in the Arctic.

For each group of samples, the frequency of occurrence of microplastics in the digestive system of benthic invertebrates was investigated and then compared between species and different feeding guilds. A conceptual diagram was created based on obtained data and a literature review to demonstrate accumulation of microplastics in the benthic ecosystem of the Pechora Sea with consideration of different feeding modes of benthic fauna. Lastly, recommendations were developed for further research and monitoring of microplastics in the Pechora Sea including recommendations on the target species, and more broadly on parameters for monitoring of the microplastic contamination of benthic ecosystems of the Arctic.

4.3. Methods

4.3.1. Sampling

RV *Kartesh* expeditions 2017–2018

Samples of benthic fauna were collected during the RV *Kartesh* expeditions during the summers of 2017 and 2018. In 2017, decapod specimens were collected from sites V1 and V2 near Vaigach Island using the *Sigsbee* bottom trawl (width 1.5 m, mesh 5 mm). The trawl was towed for 30 minutes at each site at the maximum speed of 2 knots, starting coordinates are provided in Table 3.3-1. In 2018, specimens of macrobenthic fauna were taken with the benthic grab *Okean-0.1* (capture surface 0.1 m^2) at 10 sites in the Pechora Sea (Figure 4.3-1). Coordinates of grab sampling sites provided in Table 3.3-1.

Collected species were the most abundant invertebrates in the samples and they represented different feeding guilds of macrobenthos: suspension feeders (SF) - most of the species of bivalve molluscs (*Astarte borealis*, *Astarte montagui*, *Ciliatocardium ciliatum* and *Serripes groenlandicus*); deposit feeders - *Macoma calcarea* and *Yoldia hyperborea,* and mobile omnivores (OM) - three benthic decapod species (*C. opilio*, *H. araneus* and *P. pubescens*). A total of 211 specimens of the Pechora Sea benthic fauna were collected and examined (Table 3.3.-1).

Bottom sediments from trawls and bottom grabs were washed with seawater over a 0.5 mm mesh, then decapods and bivalves were manually extracted for further analyses. Samples were preserved in buffered 4% formalin and then transferred to 70% ethanol for long-term storage.

RV *Ivan Petrov* expedition in 2008 (historic samples)

For the analyses of the temporal variation of microplastic accumulation, samples of benthic invertebrates were acquired from zoological collection of the Shirshov Institute of Oceanology, RAS, Moscow (IO RAS) in January 2019. Samples were originally collected in the Pechora Sea during the RV *Ivan Petrov* expedition in Autumn 2008. Samples of the bottom sediments were taken with the bottom grab with 0.1 m^2 capture surface, washed with the seawater over the 0.5 mm metal mesh, preserved with the 4% formaldehyde solution, transferred to 70% ethanol solution, and stored in glass jars. Specimens were pre-sorted in taxonomic groups (bivalves, polychaetes, etc) by IO RAS experts.

Common species of macrobenthos were chosen for microplastic analyses and included the following: *Astarte borealis*, *Astarte montagui*, *Ciliatocardium ciliatum*, *Macoma calcarea*, *Yoldia* *hyperborea*. A total of 73 specimens were studied from across 12 sampling sites in the central Pechora Sea (Figure 4.3-1).

RV *Akademik Mstislav Keldysh* expedition in 2019 (*AMK*-78)

To further examine spatial variability of microplastic accumulation by benthic fauna, samples were taken from other areas in the Russian Arctic, namely the Kara Sea, the Laptev Sea and the East-Siberian Sea during the 78th research expedition of the RV *Akademik Mstislav Keldysh* in September–October 2019 (*AMK*-78). Sediment samples were taken with a box corer with 0.5 m^2 capture surface (Figure 4.3-2A), washed with seawater (Figure 4.3-2B) over the 0.5 mm metal mesh (*AMK*-78 expedition report, 2019). Bivalve molluscs were manually extracted from the sediments, preserved with 4% formaldehyde solution and frozen individually. In the laboratory samples were refrozen and transferred intro 70% industrial methylated solution (IMS) solution. A total of 49 specimens from 6 sampling sites were studied (Figure 4.3-1), consisting of five species of bivalve molluscs of pan-Arctic distribution: *Astarte borealis*, *Nuculana pernula* (O. F. Müller, 1779), *Macoma calcarea*, *Mytilus edulis*, *Portlandia arctica* (Gray, 1824).

Position, water depths, sampling gear, number of species and number of specimens per each sampling site for all samples are presented in Table 4.3-1. Position of all sites is demonstrated on an overview map (Figure 4.3-1).

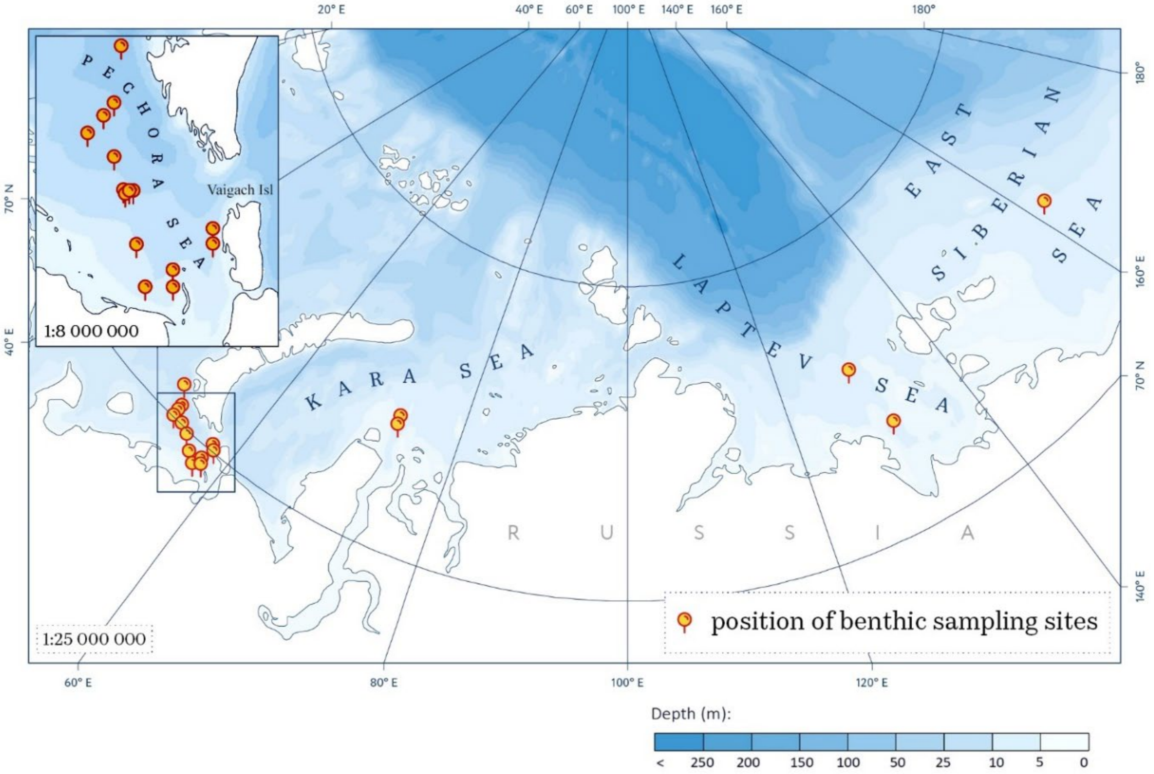


Fig. 4.3 - 1. Overview map with locations of all sites where samples of macrobenthos were collected for this study. Map courtesy of the LMSU MRC.

Table. 4.3 - 1. Synthesis table with key characteristics of all benthic sampling sites: year, position (coordinates), water depth, sampling, sampling date, number of collected specimens and number of collected species per site.

Year	Sea	Site number	Coordinates (DDM)*		Sampling gear	Sampling date (day, month, year)	Water depth, m	Number of species	Number of specimens
			N	E					
2008	Pechora Sea	1	69°37.041'	56°4.317'	Grab (*Okean-0.1*)	12.11.2008	38	3	6
2008	Pechora Sea	2	69°35.441'	56°4.728'	Grab (*Okean-0.1*)	11.11.2008	38	2	5
2008	Pechora Sea	3	69°37.744'	56°6.474'	Grab (*Okean-0.1*)	11.11.2008	36	2	3
2008	Pechora Sea	4	69°35.343'	56°3.111'	Grab (*Okean-0.1*)	12.11.2008	39	2	9
2008	Pechora Sea	7	69°36.513'	56°1.661'	Grab (*Okean-0.1*)	12.11.2008	38	3	16
2008	Pechora Sea	8	69°36.280'	56°0.506'	Grab (*Okean-0.1*)	11.11.2008	39	2	2
2008	Pechora Sea	9	69°35.969'	56°0.200'	Grab (*Okean-0.1*)	11.11.2008	39	3	9
2008	Pechora Sea	11	69°35.436'	56°1.879'	Grab (*Okean-0.1*)	12.11.2008	39	1	2
2008	Pechora Sea	12	69°35.565'	56°2.935'	Grab (*Okean-0.1*)	12.11.2008	38.5	2	5
2008	Pechora Sea	13	69°36.076'	56°3.428'	Grab (*Okean-0.1*)	12.11.2008	39	1	1
2008	Pechora Sea	15	69°36.215'	56°1.632'	Grab (*Okean-0.1*)	11.11.2008	39	1	1
2008	Pechora Sea	17	69°35.911'	56°0.762'	Grab (*Okean-0.1*)	11.11.2008	38.5	1	5
2008	Pechora Sea	19=4	69°35.343'	56°3.111'	Grab (*Okean-0.1*)	11.11.2008	39	2	3
2008	Pechora Sea	21=3	69°37.744'	56°6.474'	Grab (*Okean-0.1*)	11.11.2008	36	1	4
2008	Pechora Sea	23=1	69°37.041'	56°4.317'	Grab (*Okean-0.1*)	11.11.2008	38	1	5
2017	Pechora Sea	V1	69°52.090'	58°40.560'	*Sigsbee* trawl*	01.08.2017	39	3	53
2017	Pechora Sea	V2	69°45.628'	58°57.264'	*Sigsbee* trawl	01.08.2017	28	3	22
2018	Pechora Sea	D1	69°17.809'	58°30.986'	*Sigsbee* trawl, Grab (*Okean-50*)	24.07.2018	18	7	58
2018	Pechora Sea	D2	69°10.174'	58°49.847'	Sigsbee trawl, Grab (*Okean-50*)	25.07.2018	14	5	16
2018	Pechora Sea	MSLP2	69°15.000'	57°14.000'	Grab (*Okean-0.1*)	21.07.2018	18	3	4
2018	Pechora Sea	MV2	68°59.000'	58°12.000'	Grab (*Okean-0.1*)	23.07.2018	16	1	2
2018	Pechora Sea	NW1	69°46.000'	55°6.000'	Grab (*Okean-0.1*)	21.07.2018	52	1	1
2018	Pechora Sea	NW13	70°39.450'	52°51.107'	Grab (*Okean-0.1*)	19.07.2018	180	2	4
2018	Pechora Sea	NW7	69°45.435'	54°3.193'	Grab (*Okean-0.1*)	21.07.2018	83	1	1
2018	Pechora Sea	NW8	69°59.918'	54°0.270'	Grab (*Okean-0.1*)	21.07.2018	98	3	3
2018	Pechora Sea	NW9	70°9.773'	53°59.917'	Grab (*Okean-0.1*)	19.07.2018	112	3	9
2018	Pechora Sea	V1	69°52.090'	58°40.560'	*Sigsbee* trawl, Grab (*Okean-50*)	14.07.2018	39	8	17
2018	Pechora Sea	V2	69°45.628'	58°57.264'	*Sigsbee* trawl, Grab (*Okean-50*)	15.07.2018	28	6	21
2019	Laptev Sea	6490	73°6.503'	130°20.661'	Box-corer	06.10.2019	21	2	10
2019	Laptev Sea	6506	75°13.581'	128°38.371'	Box-corer	08.10.2019	46	3	4
2019	Kara Sea	6537	73°34.544'	73°20.177'	Box-corer	17.10.2019	20	2	9
2019	Kara Sea	6539	73°49.900'	73°14.900'	Box-corer	17.10.2019	30	1	20
2019	East-Siberian Sea	6473	74°54.268'	160°56.414'	Box-corer	01.10.2019	45.5	2	5

*Degrees, Decimal minutes (DDM)

4.3.2. Dissection and digestion

Samples were identified to species level using regional taxonomic identification keys (Gaevskaya, 1948; Naumov, 2006). Each animal was examined for presence of ingested microplastics with a combination of visual examination, digestion and dissection methods following protocols developed by Courtene-Jones et al. (2018) and La Beur et al. (2019) with adaptations. Only particles found inside the digestive system (stomach of crustaceans or visceral mass of molluscs) were considered *ingested* and were used for further analyses. Gills and mantle cavity were visually examined (Figure 4.3-2D), the presence and number of particles were noted, but particles found outside digestive systems were not used in further analyses to reduce bias from airborne contamination.

Crustaceans were dissected on board and stomachs were preserved individually in 70% ethanol. In the laboratory, stomachs were dissected, and stomach contents were visually examined under a Zeiss SteREO Discovery V20 stereomicroscope. Fragments of animals and plants identified as prey items were extracted (see Chapter 3 for more details), remains were placed in trypsin/deionised solution in a 50 mL glass covered vials in a water bath at 40°C to digest overnight (15–20 hours), then washed over a 40 µm metal strain to separate microparticles made of artificial synthetic polymers from digested organic matter of biological origin. Microparticles were then examined and photographed under a stereomicroscope and preserved in individual 5 ml glass vials. Bivalves were preserved whole until the laboratory, then air dried on filter paper until no drops of excess ethanol drops were visible, weighed (wet mass with shell) on the Jewelry Scale (ML-CF3 – reported wet mass accuracy 0.01 g), measured with Vernier callipers (length, width and height, see schema in Figure 4.3-2C), then dissected and visceral mass was placed for digestion as described above. Data on metric measurements (weight, linear – length (L), width (W), hight (H)) of each specimen are presented in the specimen catalogue in Appendix 4-1.

4.3.3. Data analysis

For each specimen, presence/absence of microplastic particles was noted, as well as their abundance and location in the body (stomach/gills for crustaceans; digestive system/mantle cavity/ctenidium for molluscs). A presence/absence data matrix of ingested microparticles was then used to calculate the frequency of occurrence of microplastics across sampling sites, species and feeding guilds.

Pearson correlation was used to test relationships between microplastics abundance and weight and size (length) of organisms. Multiple proportion confidence intervals (CI) were calculated using the Clopper-Pearson method and plotted in a box plot to assess differences of accumulation of microplastics between species collected in the same year.

To assess differences in accumulation of microplastics by different species, the non-parametric Kruskal-Wallis test was applied. To assess differences between groups of species (feeding guilds) or groups of sampling sites, the non-metric multidimensional scaling (nMDS) and the cluster analysis based on an unweighted pair group method with arithmetic mean (UPGMA) algorithm based on the Bray-Curtis similarity index were used. Then a one-was analysis of similarities (ANOSIM) was used for pairwise comparisons of the groups of sampling sites / species. P-values of each pair were given, with sequential Bonferroni corrections applied. Similarity Percentage (SIMPER) analysis was used to assess contribution of individual species to dissimilarities. For the species that occurred in the Pechora Sea both in 2008 and in 2017–2018, risk difference was calculated to assess importance of inter-year variability of microplastic accumulation based on Pearson's Chi-squared as follows:

Risk difference: $\mathrm{RD} = p_1 - p_0$

95% **confidence interval** on risk difference Pearson's chi-squared):

$$S_e = \sqrt{\frac{p_1(1-p_1)}{n_1} + \frac{p_0(1-p_0)}{n_0}}$$

Where n_1=d_1+h_1, n_0=d_0+h_0 and p_1=d_1/n_1, p_0=d_0/n_0 and d_1 refers to the outcome 1 of treatment 1; h_1 refers to outcome 2 of treatment 1; d_0 refers to outcome 1 of treatment 2, and h_0 refers to outcome 2 of treatment 2.

A Chi-squared test based on frequency data was also used to assess the strength and statistical significance of any association between regional seas and occurrence of ingested microplastics (with significant differences set at p<0.05). All statistical calculations were performed using the free statistical software PAST version 3.22 (Hammer and Harper, 2006).

Fig. 4.3 - 2. Overview of methods of microplastic sampling (A) Deployment of the box corer onboard expedition *AMK*-78, photo courtesy of Vyacheslav Volodin; (B) Washing of the sediments, photo courtesy of Anastasia Zagovenkova; (C) Schema of morphometric measurements of the bivalve mollusc *Astarte borealis*, L – length; W – width; H – hight; (D) Microplastic fibre inside the mantle cavity.

4.3.4. Quality assurance / quality control (QA/QC)

To prevent contamination of samples, number of steps were taken during the sample collection and in laboratory. Onboard, all equipment and jars were rinsed with pre-filtered Milli-Q water before use (0.45 µm filters) and all consumables were taken directly from the packaging. Samples were stored in sealed glass jars. In addition, during the AMK-78 cruise, field blanks were performed for a ship-board underway pump-trough system (n=3), full methods presented in Yakushev et al. (2021).

Laboratory quality control measures to reduce artificial contamination of samples were adopted from Courtene-Jones et al. (2018) and included the following: only 100% cotton laboratory coats were used for the duration of the study; the working area was cleaned with IMS solution prior to any analysis; dissection kit and tools were cleaned with IMS then triple-rinsed in deionised water before used. A control uncovered petri dish with damp Whatman filters was placed in the fume hood and on the working surface outside the fume hood to identify potential airborne contaminants with various exposure times, total n=8 and then studied under stereo microscope for potential microplastic contamination (Woodall et al., 2015).

4.4. Results

4.4.1. Contamination control

No microplastic fibres were found on the filters (damp Whatman filters) left inside the fume hood exposure time 3 hours, 6 hours, 12 hours, 24 hours (n=4). Two white fibres were identified on the filter left on the working surface outside the fume hood after 24 hours of exposure. No fibres were identified on the filters left on the working surface after 30 mins or 1 hour of exposure (n=2). No contamination was found on the field blanks. Considering that samples were never left uncovered outside the fume hood for over 30 minutes (maximum dissection time) for the entire duration of study, background contamination was considered negligible for this study (Torre et al., 2016; La Beur et al., 2019).

4.4.2. Occurrence of ingested microplastics in macrobenthos

RV *Kartesh* expeditions 2017–2018

In total, 95 microparticles were found in 211 examined specimens collected in 2017–2018. All microparticles were classified as microfibers. Out of all microfibers, 71 were in stomachs, whereas 24 microfibers were in other organs (gills, mantle, or mantle cavity). A total of 62 specimens contained microplastics in their digestive systems (1–3 microfibres per specimen). No correlation was found between the abundance of microplastics and size (maximum length) of specimens (R=-0.02; p=0.68), or weight (total wet weigh) of specimens (R=-0.07; p=0.32).

Individuals of 13 species of free-living invertebrates were studied, representing five feeding guilds. Suspension feeders were most abundant (six species of bivalve molluscs *Astarte borealis*, *Astarte eliptica*, *Astarte montagui*, *Ciliatocardium ciliatum*, *Serripes groenlandicus*, *Mytilus edulis*), followed by mobile benthic omnivores (three species of decapod crustaceans *Chionoecetes opilio*, *Hyas araneus*, *Pagurus pubescens*) and a diverse group of deposit-feeder molluscs with slightly different feeding strategies: surface deposit feeder (*Macoma calcarea*); subsurface deposit feeders (*Yoldia hyperborea* and *Nuculana pernucula*) and grazer / deposit feeder gastropod (*Margarites groenlandicus*).

RV *Ivan Petrov* expedition in 2008 (historic samples)

A total of 73 specimens of benthic invertebrates collected in 2008 across 12 sites in the Pechora Sea were available for this study. Twenty-nine microfibres were found, of which 10 occurred inside stomachs and rest were found in mantle cavity or on the surface of gills. Seven individuals had ingested microplastics in their stomachs (1–2 microfibres per specimen). Abundance of ingested microplastics showed no dependence on the mass of specimens (R=-0.12; p=0.37), or their size (maximum length) (R=-0.07; p=0.59).

Five species of bivalve molluscs were studied, divided into suspension feeders (*Astarte borealis*, *Astarte montagui*, *Ciliatocardium ciliatum*) and deposit feeders (surface deposit feeder *Macoma calcarea* and a subsurface deposit feeder *Yoldia hyperborea*). All study species were common in the research area and were also present in the 2017–2018 samples.

RV *Akademik Mstislav Keldysh* expedition in 2019 (*AMK*-78)

Forty-nine specimens were collected from the Kara, Laptev and East Siberian Seas in the Russian Arctic in September–October to compare levels of microplastic accumulation in these areas with the Pechora Sea. A total of 21 microfibers were detected, of which 18 were found inside the stomachs of 13 specimens (1–4 fibres per stomach). Additional two fibres were found inside the mantle cavity and one fibre on the gills. Abundance of ingested microplastic did not show correlation with size (length) of specimens (R=0.2; p=0.10) but it did show a positive correlation with weight of specimens (R=0.3; p=0.02).

Six bivalve species were present in the samples, these represented suspension feeders (*Astarte borealis, Mytilus edulis*), and deposit feeders (*Macoma calcarea*, *Yoldia hyperborea and Portlandia arctica*). All of these species were also found in the Pechora Sea, except for *Portlandia arctica*, a common bivalve of the Yoldiidae family that has a pan-Arctic distribution including the Pechora Sea but due to high spatial variability of macrobenthic communities in the Pechora Sea was absent in the research area.

A matrix of all specimens with a total number for each year, each sampling site and each feeding guild, and number of specimens with ingested microplastics is presented in Table 4.4-1.

Table. 4.4 - 1. A matrix with number of individuals of each species studied per site per year. In brackets is the number of specimens with ingested microplastics.

Species **Sampling site**	***A. borealis***	***A. elliptica***	***A. montagui***	***C. ciliatum***	***M. edulis***	***S. groenlandicus***	***M. calcarea***	***N. pernula***	***Y. hyperborea***	***P. arctica***	***M. groenlandicus***	***C. opilio***	***H. araneus***	***P. pubescens***
Feeding guild*	**SF**						**DF**				**G/ DF**	**Om**		
2017–2018														
D1	7(2)	0	2(1)	2(0)	0	6(3)	7(1)	1(0)	33(7)		0	0	0	0
D2	1(1)	1(1)	12(5)	0	0	1(0)	0	0	0		1(0)	0	0	0
MSLP2	0	0	0	0	0	2(0)	0	1(1)	0		1(0)	0	0	0
MV2	2(0)	0	0	0	0	0	0	0	0		0	0	0	0
NW1	1(0)	0	0	0	0	0	0	0	0		0	0	0	0
NW13	0	0	3(0)	0	0	0	0	0	1(0)		0	0	0	0
NW7	1(0)	0	0	0	0	0	0	0	0		0	0	0	0
NW8	2(0)	1(1)	0	0	0	0	0	0	0		0	0	0	0
NW9	5(2)	0	2(2)	2(0)	0	0	0	0	0		0	0	0	0
V1	1(0)	1(1)	7(2)	2(1)	0	1(0)	3(1)	1(0)	1(0)		0	3(1)	6(2)	13(5)
V2	1(1)	2(0)	10(4)	4(0)	1(1)	3(1)	0	0	0		0	20(7)	3(0)	30(8)
Total	21(6)	5(3)	36(14)	10(1)	1(1)	13(4)	10(2)	3(1)	35(7)		2(0)	23(8)	9(2)	43(13)
2008														
1(23)	2(1)		0	3(0)			6(0)		0					
2	1(0)		0	3(0)			0		0					
3(21)	1(0)		0	2(0)			4(0)		0					
4(19)	4(0)		0	1(0)			7(1)		0					
7	0		1(0)	0			13(1)		1(1)					
8	1(0)		0	0			0		0					
9	2(1)		3(1)	0			4(1)		0					
11	2(0)		0	0			0		0					
12	1(0)		0	4(0)			0		0					
13	0		0	1(0)			0		0					
15	0		0	1(0)			0		0					
17	0		0	0			5(0)		0					
Total														
2019														
6473	0				2(1)		0	0		3(0)				
6490	0				0		1(0)	0		9(2)				
6506	2(1)				0		1(1)	1(0)		0				
6537	0				0		2(1)	0		8(1)				
6539	0				0		0	0		20(6)				
Total														

*SF – suspension feeder; DF – deposit feeder; G – grazer; Om - omnivores

4.4.3. Variation in microplastic ingestion between macrobenthic species

The average frequency of occurrence of ingested microplastics for all studied species was estimated as number of specimens with ingested microplastics divided by total number of studied specimens of this species and estimated as 27±6% ranging from 4% for bivalve *C. ciliatum* to 38% in another suspension feeding bivalve mollusc *A. montagui*. Only species represented by ≥5 individuals were used for analyses to reduce bias. None of the studied species were free of plastic pollution with a minimum of one stomach containing ingested microplastics in each of the species.

A diagram of occurrence of ingested microplastics per species per year is presented in Figure 4.4-1. The number of specimens with ingested microplastics is shown in red and number of specimens free of microplastics – in blue.

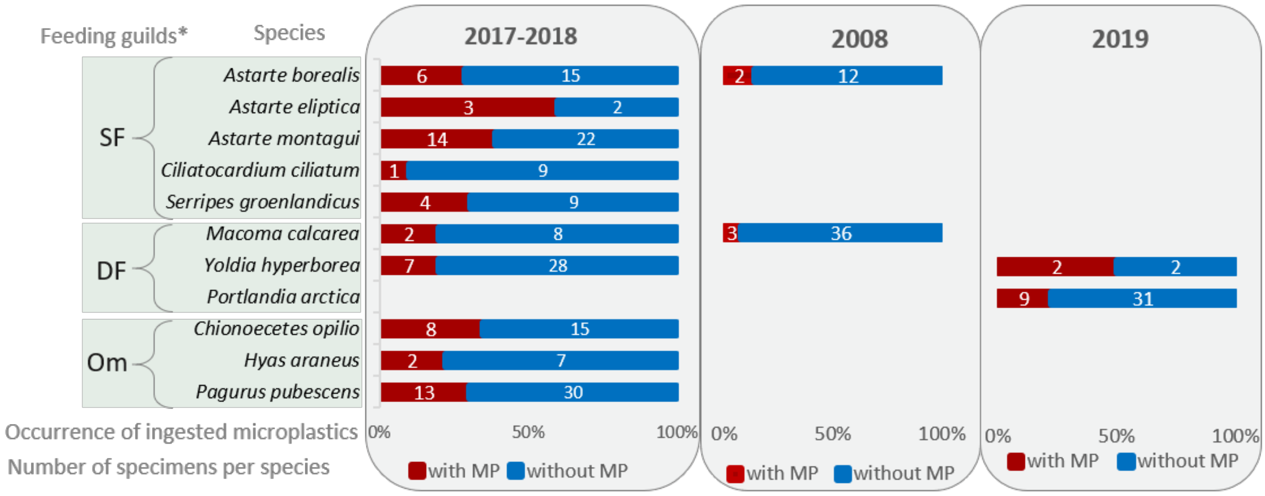


Fig. 4.4 - 1. Diagram of occurrence of ingested microplastics in benthic fauna from different feeding guilds for all studied samples.

*SF – suspension feeder; DF – deposit feeder; Om – omnivores
MP – microplastics

A Whiskers plot in Figure 4.4-2 shows the occurrence of ingested microplastics for each species with multiple proportion 95% confidence intervals calculated using the Clopper-Pearson method. Whiskers clearly overlapped between most of the species, the only pair that could be distinguished by this method were *A. montagui* and *C. ciliatum* that correspond to the highest and the lowest occurrence of ingested microplastics, respectively.

Non-parametrical Kruskal-Wallis test for equal medians did not identify significant differences in ingested microplastics occurrence between the species (p=0.22; H (ch^{i2})=5.356; H_c (tie corrected)=7.009).

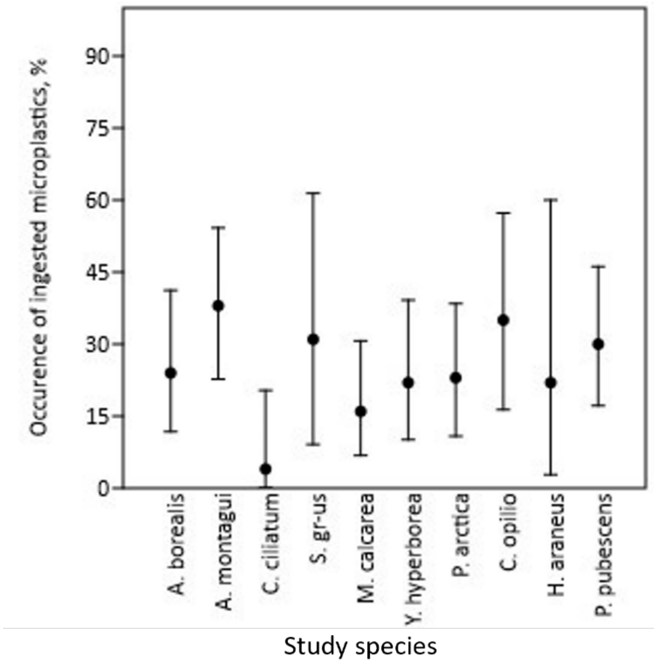


Fig. 4.4 - 2. Whiskers plot for occurrence of ingested microplastics (%) and multiple proportion 95% confidence intervals (CIs) in different species (n>5) of macrobenthos calculated using the Clopper-Pearson method based on proportions given as % and sample size.

*S.g-us – *Serripes groenlandicus*

4.4.4. Variation in microplastic ingestion between feeding guilds of macrobenthos in the Pechora Sea

The study species represented a variety of feeding strategies, namely suspension feeders (SF), surface deposit feeders (SDF), subsurface deposit feeders (SSDF), grazers (G) and mobile omnivores (Om), or a combination of those (e.g., mixed SF/SDF, or mixed G/DF). For simplicity of further analyses these strategies were generalized into three major groups: suspension feeders (SF), deposit feeder (DF) and omnivores (Om). Table 4.4-2 demonstrates mean frequencies of occurrence of ingested microplastics for each feeding guild for each year (only species with n≥5 were taken into account).

Table. 4.4 - 2. Comparison of occurrence of ingested microplastics by different feeding guilds in different years (number of specimens is shown in brackets for each value)*.

Years	**Feeding guilds**		
	SF	**DF**	**Om**
2008	7% (n=29)	8% (n=39)	-
2017–2018	34% (n=85)	20% (n=45)	29% (n=75)
2019	-	23% (n=40)	-

*SF – suspension feeder; SDF – surface deposit feeder; SSDF – subsurface deposit feeder; G – grazer; Om – omnivores

Values of microplastic occurrence for each feeding guild altered between the years of sampling with no consistent pattern. To investigate differences between the feeding guilds in more detail, data from 2017–2018 years from the Pechora Sea was used to calculate ANOSIM and nMDS (Table 4.4-3).

Table. 4.4 - 3. Data on microplastic ingestion by species from different feeding guilds in the Pechora Sea in 2017–2018, used for comparison of the feeding guilds*

Sites / species	D1	D2	NW8	NW9	V1	V2	Feeding guilds
Astarte borealis	0.28	1	0	0.4	0	1	**SF**
Astarte eliptica	0	1	1	0	1	0	**SF**
Astarte montagui	0.5	0.41	0	1	0.28	0.4	**SF**
Ciliatocardium ciliatum	0	0	0	0	0.5	0	**SF**
Serripes groenlandicus	0.5	0	0	0	0	0.33	**SF**
Macoma calcarea	0.14	0	0	0	0.33	0	**DF**
Yoldia hyperborea	0.21	0	0	0	0	0	**DF**
Chionocetes opilio	0	0	0	0	0.33	0.35	**Om**
Hyas araneus	0	0	0	0	0.33	0	**Om**
Pagurus pubescens	0	0	0	0	0.38	0.27	**Om**

*SF – suspension feeder; DF – deposit feeder; Om – omnivores

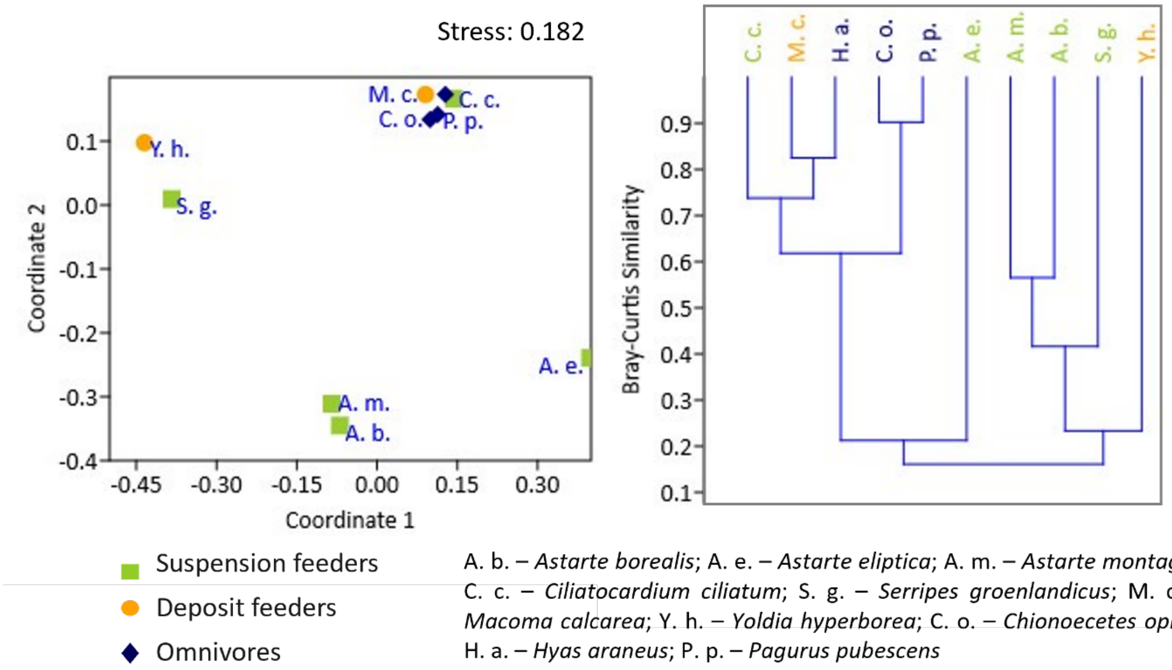
Pairwise comparisons between the feeding guilds with ANOSIM analysis did not reveal statistically significant differences in any pair of the feeding guilds in accumulation of microplastics (all p>0.05) (Table 4.4-4).

Table. 4.4 - 4. Pairwise comparison of the feeding guilds with ANOSIM analysis, Bonferroni-corrected p values and R values showed for each pair.

	DF	Om
SF	p=0.72; R=0.2	p=0.6927; R=0.1
DF		p=0.2991; R=0.58

*SF – suspension feeder; DF – deposit feeder; Om – omnivores

Plotting groups of species based on frequencies of ingested microplastics data with nMDS or cluster analyses has also shown that feeding guilds did not form separate groups (Figure 4.4-3). Both in nMDS plot and in UPGMA cluster graph species from different feeding modes appear together, for example *C. ciliatum* (suspension feeder), *M. calcarea* (predominantly deposit feeder) and *H. araneus* (omnivores). Overall, no statistical differences in occurrence of ingested microplastics were found between the feeding guilds of macrobenthic invertebrates in the Pechora Sea.



A. b. – *Astarte borealis*; A. e. – *Astarte eliptica*; A. m. – *Astarte montagui*; C. c. – *Ciliatocardium ciliatum*; S. g. – *Serripes groenlandicus*; M. c. – *Macoma calcarea*; Y. h. – *Yoldia hyperborea*; C. o. – *Chionoecetes opilio*; H. a. – *Hyas araneus*; P. p. – *Pagurus pubescens*

Fig. 4.4 - 3. Groups of species based on nMDS (on the left), and UPGMA hierarchical cluster analysis (on the right), both calculated with Bray-Curtis similarity measure. Different feeding guilds are represented by different colours: (1) Suspension feeders – green; (2) Deposit feeders – orange; (3) Omnivores – blue.

4.4.5. Variation of microplastic ingestion between sampling sites in the Pechora Sea

To assess whether ingestion of microplastics varied across the sampling sites in the Pechora Sea same data set was used as for the assessment of the differences between the feeding guilds (Table 4.4-3). Ingested microplastics were identified at six out of 11 sampling sites sampled in 2017–2018, namely D1, D2, V1, V2, NW9 and NW8. The number of specimens per sites varied greatly from three specimens (site NW8) to 70 specimens from site V1. Differences in the number of available samples were related to different sampling techniques (grab and trawl) and to high variability in abundance and biomass of benthic communities in the area (Denisenko et al., 2019). Average occurrence of ingested microplastics across the sites were compared using the non-parametric Kruskal-Wallis test and no significant difference between sample medians was identified (p>0.05) (Table 4.4-5).

Table. 4.4 - 5. Kruskal-Wallis test for equal medians applied for average occurrence of ingested microplastics across the sites in the Pechora Sea in 2017–18.

Kruskal-Wallis test for equal medians	Values
H (chi^2):	11.22
H_c (tie corrected):	14.68
p (same):	0.1002

The total number of specimens with microplastics per sampling site was positively correlated with size of the sample per sampling site (R=0.96; p=0.0015; N_{total}=198; N_{withMP}=61). Based on their geographic position, sampling sites could be divided into three groups: (1) NW8 and NW9 – sites in the central open-water area of the Pechora Sea at the depth range 100–110 m, (2) V1 and V2 near the west coast of Vaigach Island, 30–40 m; (3) D1 and D2 near Dolgy Island, 14–18 m (Figure 4.3-1). Despite clear differences in location and topography between the groups of sampling sites, ANOSIM analysis has not revealed any differences between the groups (all p>0.05) (Table 4.4-6).

Table. 4.4 - 6. Pairwise comparison of the groups of sampling sites with ANOSIM analysis, Bonferroni-corrected p values and R values showed for each pair.

	NW	**V**
D	p=1; R=-0.62	p=1; R=-0.5
NW		p=1; R=-0.37

*D, NW, V – site codes

Similarly, the nMDS plot and UPGMA clusters showed that sampling sites which were geographically close did not show any similarity in occurrence of ingested microplastics (Figure 4.4-4).

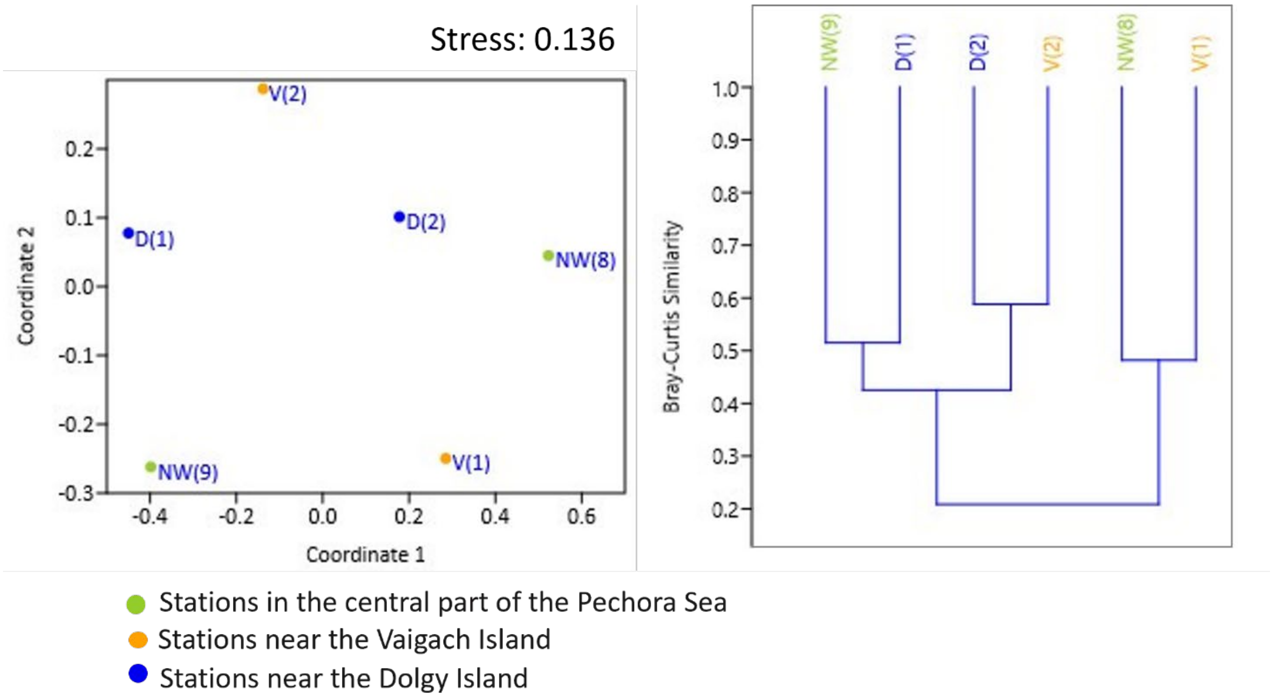


Fig. 4.4 - 4. Sampling sites plotted with nMDS (on the left), and UPGMA hierarchical cluster analysis (on the right), both calculated with Bray-Curtis similarity measure. Different colours represent sampling sites that are geographically close: (1) Green – sampling sites in the deeper open-water central area of the Pechora Sea; (2) Orange – sampling sites near Vaigach Island; (3) Blue – shallow-water sampling sites near Dolgy Island.

4.4.6. Microplastic ingestion in different Seas of the Eurasian Arctic

During the *AMK*-78 expedition in 2019, additional samples were taken from the Kara, Laptev and East-Siberian Seas of the Arctic Ocean. Microplastics ingested by benthic fauna were discovered in all studied areas. Interestingly, mean occurrence of ingested microplastics were very close between those areas with only 4% difference between the maximum level discovered for the Pechora Sea and the Laptev Sea (29%) and the lowest level found in the East-Siberian Sea (25%) (Table 4.4-7). Average rate of occurrence of ingested microplastic for the entire dataset estimated as 27±2%.

Table. 4.4 - 7. Occurrence of ingested microplastics in different areas of the Eurasian Arctic: the Pechora Sea, the Kara Sea, the Laptev Sea, the East-Siberian Sea.

	N total	N with MP	Occurrence
Pechora Sea (2017–2018)	211	62	29%
Kara Sea (2019)	30	8	27%
Laptev Sea (2019)	14	4	29%
East-Siberian Sea (2019)	4	1	25%

*MP – microplastics; N – number

Further statistical tests were not performed to assess differences between the seas due to the small sample size available for this study – as only one species in the dataset had n≥5 (shown in bold) (Table 4.4-8).

Table. 4.4 - 8. Specimens from the Kara Sea, the Laptev Sea and the East-Siberian Sea – feeding guilds, total number and number with ingested microplastics. Species with n≥5 highlighted in bold.

Species	Feeding Guild	Total	With Plastic
Astarte borealis	Suspension feeder	2	1
Macoma calcarea	Suspension feeder/Surface deposit feeder	4	2
Mytilus edulis	Suspension feeder	2	1
Nuculana pernula	Subsurface deposit feeder	1	0
Portlandia arctica	**Subsurface deposit feeder**	**40**	**9**

4.4.7. Temporal variation of microplastic ingestion by macrobenthos in the Pechora Sea

Five species of macrobenthos occurred in both 2008 and 2018, three of them also had n≥5 allowing assessment of inter-annual variability of microplastics accumulation in these species: *Astarte borealis*, *Ciliatocardium ciliatum* and *Macoma calcarea*. Occurrence of ingested microplastics was different between years in each of these species (Table 4.4-9). Overall, the level of microplastic occurrence was mean 9% in 2008 and mean 29% in 2018.

Table. 4.4 - 9. Occurrence of ingested microplastics in stomachs of bivalve species in 2008 and 2018 and increase in microplastic occurrence for each species.

	2008	**2018**	**Increase in microplastic occurrence**
	Occurrence of ingested microplastics		
Astarte borealis	14% (n=14)	29% (n=21)	2.07
Ciliatocardium ciliatum	0% (n=15)	10% (n=10)	10
Macoma calcarea	8% (n=39)	20% (n=10)	2.5

To test statistical significance of temporal variability, Chi-squared test was applied (Table 4.4-10). Overall, differences were statistically significant for (1) all samples available in 2008 vs all samples available in 2018; (2) all samples available in 2008 vs all samples available in 2017+2018; (3) cluster of reoccurring species (*A. borealis*; *A. montagui*, *C. ciliatum*, *M. calcarea*, *Y. hyperborea*) in 2008 vs 2018. However, when each species was analysed individually, no statistical differences were confirmed between 2008 and 2018 for any of the species (Table 4.4-10).

Table. 4.4 - 10. Outcomes of the Chi-squared test for differences between the years of sampling. For each compared category, number of samples with and without microplastics shown; for each test p-values, Chi-squared values and risk differences (RD) values provided. Statistically significant p-values (p<0.05 are marked with green shading).

Categories	**N with MP**	**N without MP**	**RD**	**Chi-squared**	**p**
All samples					
2008	7	66	-0.19	10.08	0.0014
2018	39	97			
All samples					
2008	7	66	-0.19	11.67	0.0006
2018+2017	62	148			
Only re-occurring species (*A. borealis*; *A. montagui*, *C. ciliatum*, *M. calcarea*, *Y. hyperborea*)					
2008 (5 species)	7	66	-0.17	8.16	0.0042
2018 (5 species)	30	82			
Astarte borealis					
2008	2	12	-0.14	0.97	0.3241
2018	6	15			
Ciliatocardium ciliatum					
2008	0	15	-0.1	1.56	0.2113
2018	1	9			
Macoma calcarea					
2008	3	36	-0.12	1.31	0.2513
2018	2	8			
2018	7	28			

*MP – microplastics; RD – risk difference; N – number

Pairwise comparison of the occurrence of ingested microplastics between the years with ANOSIM also proved a statistically significant difference between 2008 and 2017–18 (R=0.46; p=0.008), and visualisation of the sampling sites with nMDS plot allowed to distinguish groups of sampling sites sampled in 2008 and 2017–18 respectively (Figure 4.4-5).

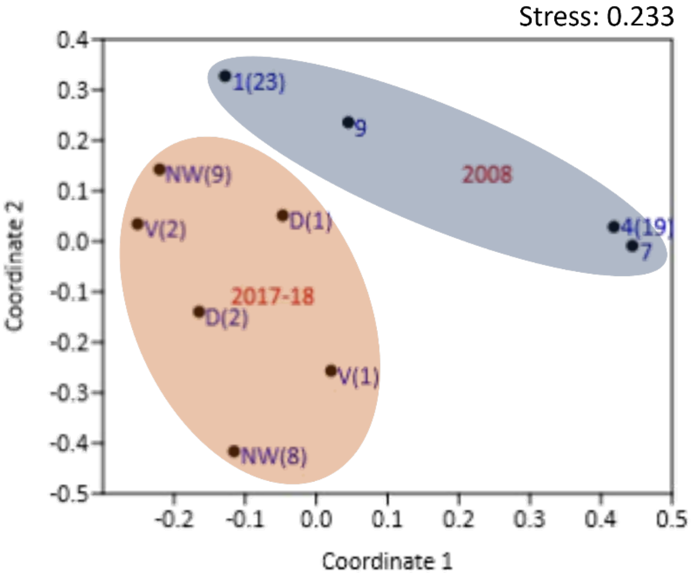


Fig. 4.4 - 5. Sampling sites plotted with nMDS, sampling sites sampled in 2008 showed in blue oval, sites from 2017–18 – in orange oval.

Outcomes of the SIMPER analysis showed an overall average dissimilarity 71.11% between the years with the greatest contributions to dissimilarity from *A. borealis* (61%) and *M. calcarea* (28%) (Table 4.4-11).

Table. 4.4 - 11. Occurrence of ingested microplastics in stomachs of bivalve species in 2008 and 2018 and increase in microplastic occurrence for each species.

Taxon	Average dissimilarity	Contrib. %	Cumulative %	Mean 2017–2018	Mean 2008
Astarte borealis	43.79	61.58	61.58	0.447	0.25
Macoma calcarea	19.97	28.09	89.67	0.0783	0.115
Ciliatocardium ciliatum	7.348	10.33	100	0.0833	0

Overall, the tests proved statistically significant differences in the occurrence of ingested microplastics between 2008 and 2017–18, and average rate of microplastic ingestion observed in macrobenthos in the Pechora Sea was three times higher in 2018 than 10 years before.

4.5. Discussion

4.5.1. Variability in microplastic accumulation

Biological variability

Differences in accumulation of ingested microplastics between species can be theoretically attributed to their size, age and feeding behaviour. Data from the present study do not provide enough evidence to investigate such differences in detail. No correlation between abundance of microplastics and size (expressed as length) (R=-0.03; p=0.51) or mass (proxy of age) (R=-0.08; p=0.16) were found. Similarly, a previous study in the North Atlantic showed that abundance of ingested microplastics in macrobenthos did not vary with length, mass or feeding mode (Courtene-Jones et al., 2017). Many studies on microplastic ingestion in benthos have not tested any relationship between length/mass of organisms and abundance of ingested microparticles (Taylor et al., 2016; Fang et al., 2018; La Beur et al., 2019).

Occurrence of plastic ingestion varied between study species and feeding guilds with no visible patterns and relations between the occurrence of ingested microplastics and feeding behaviour. Most of macrobenthos in the research area were susceptible to microplastic contamination to some extent – out of the 14 study species only one with the smallest sample size was free of microplastics. Previous studies showed contradictory results regarding differences of microplastic ingestion between feeding guilds of macrobenthos. Taylor (et al., 2016) predicted that deposit feeders might be more vulnerable to microplastic load than suspension feeders. In the present study, suspension feeders had similar occurrence of ingested microplastics than deposit feeders in the Pechora Sea and in the other areas of the Eurasian Arctic. In benthic omnivores (the snow crab, the spider crab and hermit crabs) the ingestion rate of microplastics was near the values for suspension feeders at 31%. Bivalves, both deposit and suspension-feeding, are primary consumers extracting organic matter from the water column and/or detritus layer on sediments. Benthic decapods are higher-level consumers actively preying or scavenging on organisms at the seafloor and have complex diets. Therefore, in addition to microplastics from the substrate, benthic decapods also passively ingest particles accumulated in the prey (Taylor et al., 2016), which might result in increased ingestion of microplastic occurrence compared to filter, deposit, or suspension feeders. However, there is very little information available on physiological accumulation of microplastics in digestive systems and other organs and tissues of organisms after ingestion. It is not unlikely, that some species accumulate microplastics more than others after ingestion, but this requires detailed investigation into physiology of feeding mechanisms and anatomy of digestive systems of those species.

Overall, this study agrees with some of the previous studies in that there were no statistically significant differences in frequency of microplastic ingestion between feeding guilds (Courtene-Jones et al., 2018; La Beur et al., 2019).

It was notable that the snow crab *C. opilio* had a higher frequency of occurrence of microplastics than other decapod species and the second highest overall of all study species with n>5 (35%). As shown in Chapter 3, *C. opilio* has an overlapping diet with the spider crab *H. araneus* and hermit crab *P. pubescens*, but it tends to show more diverse diets and accumulate more types of prey items in their stomach contents compared to other benthic decapods in the Pechora Sea. There is currently no evidence of accumulation or translocation of microplastics by benthic crustaceans, as opposed to bivalves that have shown ingested plastics being capable of translocating to circulatory systems (Browne et al., 2008). Nevertheless, presence of ingested microplastics in stomachs of *C. opilio* is certainly a food security concern as it is a commercially exploited seafood species in the Russian sector of the Barents Sea and therefore passive consumption of microplastics by humans from *C. opilio* is possible with unknown consequences to human health.

Spatial variability

In addition to by far the most comprehensive dataset on microplastic ingestion by macrobenthos in the Pechora Sea, this study also provides early data for the Kara Sea, the Laptev Sea and the East-Siberian Sea. Clearly, microplastic contamination in the Pechora Sea is not a unique phenomenon in the Arctic, ingested microplastics were found in benthic organisms in each of the study areas. The few samples available from the other study regions did not allow statistical analyses to compare data, however these observations provide first insights into microplastic contamination of the broader Arctic Ocean. It has been shown for the Pechora Sea that abundance of microplastics was related to sample size (total number of animals per sampling site) ($p=0.0006$), rather than location, which is why bigger and standardized samples are needed from the other regions to investigate differences between regions in microplastic accumulation.

Direct comparison with the results of previous studies is also complicated due to different quantitative expressions of microplastic occurrence and different sampling sizes. However, it can be noted, that ingested microplastics were also previously found in the Chukchi Sea of the Arctic Ocean, the Bering Sea in the North Pacific (Fang et al., 2018) and in the North Atlantic (Courtene-

Jones et al., 2018; La Beur et al., 2019) (Table 4.5-1). A recent study in the Chukchi-Bering Sea shelf has provided overall estimations of abundance of ingested microplastics, without dividing into geographical regions (Fang et al., 2018).

Table. 4.5 - 1. Comparison of occurrence of ingested microplastics in different geographical regions of the Arctic and sub-Arctic, based on this study and literature review.

Geographic region	Source of data	Year of sampling	Occurrence of ingested microplastics
Pechora Sea	Present study	2017–2018	29% (n=211)
Kara Sea	Present study	2019	27% (n=30)
Laptev Sea	Present study	2019	29% (n=14)
East-Siberian Sea	Present study	2019	25% (n=4)
Chukchi Sea	Fang et al., 2018	2017	0.02 to 0.46 items g^{-1} wet weight (ww) (n=413)
Bering Sea (North Pacific)	Fang et al., 2018		
Mingulay Reef (North Atlantic)	La Beur et al., 2019	2009	11% (n=112)
Rockall Trough (North Atlantic)	Courtene-Jones, 2017	2016	48% (n=66)

The results of the *AMK*-78 (2019) expedition provide first results on the concentrations of microplastics in the surface and subsurface (3 m) water in the Barents, Kara, Laptev and East-Siberian Seas (Yakushev et al., 2021) (Table 4.5-2). Similarly to the ingested microplastics, floating microplastics were found in all the studied areas and their concentrations varied greatly between the seas (Yakushev et al., 2021). It was shown that microplastics in the surface and subsurface water likely have different origins: whereas particles found at the surface are linked to the low-saline plumes formed by the discharge of the Great Siberian Rivers, microplastics in the sub-surface likely originate from surface Atlantic water, brought to the Arctic with the thermohaline circulation (Yakushev et al., 2021). This was reflected in the mass concentrations in the subsurface waters with largest values in the Barents Sea (6.6 μg/m^3) where the influence of inflow from the North Atlantic is the strongest. This influence then gradually decreases eastwards reaching lowest values in the East-Siberian Sea (0.4 μg/m^3). Occurrence of microplastics in benthic organisms in the same areas did not follow a similar pattern, suggesting that accumulation of microplastics at the seafloor is driven by different mechanisms than in the water column. This is supported by the recent study in the Mediterranean Sea suggesting that accumulation of microplastics in the benthic ecosystems and particularly deep-sea biomes, is controlled by bottom thermohaline circulation and topography (Kane et al., 2020).

Table. 4.5 - 2. Comparison of microplastics concentrations in different geographical regions of the Arctic and sub-Arctic, based on this study and literature review.

	Surface water			Subsurface water			Macrobenthos	
	n of samples	Average n/m^3 (n/km^2)	Average ug/m^3	n of samples	Average n/m^3	Average ug*/m^3	n of samples	Occurrence of MP, %
Pechora Sea	n/a						211	29%
Yakushev et al., 2021								
Barents Sea	7	0.005 (1000)	12.5	6	0.8	6.6		
Kara Sea	15	0.003 (700)	3.8	16	1.0	1.1	30	27%
Laptev Sea	20	0.002 (400)	0.5	20	0.7	0.5	14	29%
East-Siberian Sea	6	0.010 (2000)	3.9	18	0.8	0.4	4	25%

*MP – microplastics; n – number

Within the Pechora Sea, the largest number of ingested particles (site V1) corresponded to the area with the known highest biomass of macrobenthic communities (Denisenko et al., 2019), an area that also likely serves as a foraging ground for the local population of Atlantic walrus (Semenova et al., 2019).

Overall, larger sampling sizes are needed to analyse the spatial distribution of microplastic contamination in the Arctic better, whereas the present study provides the first data on presence of ingested microplastics in benthic fauna of the Pechora Sea, the Kara Sea, the Laptev Sea and the East-Siberian Sea.

Temporal variability

This study provides the first evidence of increased accumulation of microplastics by benthic invertebrate overtime – occurrence of ingested microplastics in the Pechora Sea in 2017–2018 (29%) were significantly higher than in 2008 (9%) supported by strong statistical difference identified by Chi-square (p=0.0014) and ANOSIM (p=0.008) tests. This is an important finding suggesting that year of data collection needs to be considered to allow comparison of outcomes of different studies. No previous studies were found of ingested microplastics assessing temporal variability. On the global scale annual production of plastics has increased from 245m t (million metric tons) in 2008 to 359m t in 2019 (Plastics Europe, 2020), and it therefore can be predicted that levels of microplastic pollution are also increasing, and the occurrence of ingested microplastics in benthic ecosystems. However, more data on both inflow of plastics in the oceans and uptake by benthic fauna are needed to estimate at what rates those changes occur at. Strengthening monitoring and research to improve current level of knowledge on plastic litter in the Arctic, observe trends and identify the impacts of plastics on marine biota and human health is listed as one of key actions by the Reginal Arctic Plan on marine litter in the Arctic by the Arctic

Council (PAME, 2021). Integrating monitoring of plastics and microplastics into the long-term monitoring of plastics would allow collection of time-series data essential for analysis of temporal variability of plastic pollution.

4.5.2. Conceptual diagram of microplastic accumulation in the Pechora Sea

This study showed that some macrobenthic fauna of the Pechora Sea accumulates ingested microplastics at an average rate of occurrence in stomachs at 29% (at present). This study presents first evidence of microplastics in benthic invertebrates in the Pechora Sea. A conceptual diagram of microplastic ingestion by benthic fauna in the Pechora Sea, based on the findings of this study and literature review, is presented in Figure 4.5-1.

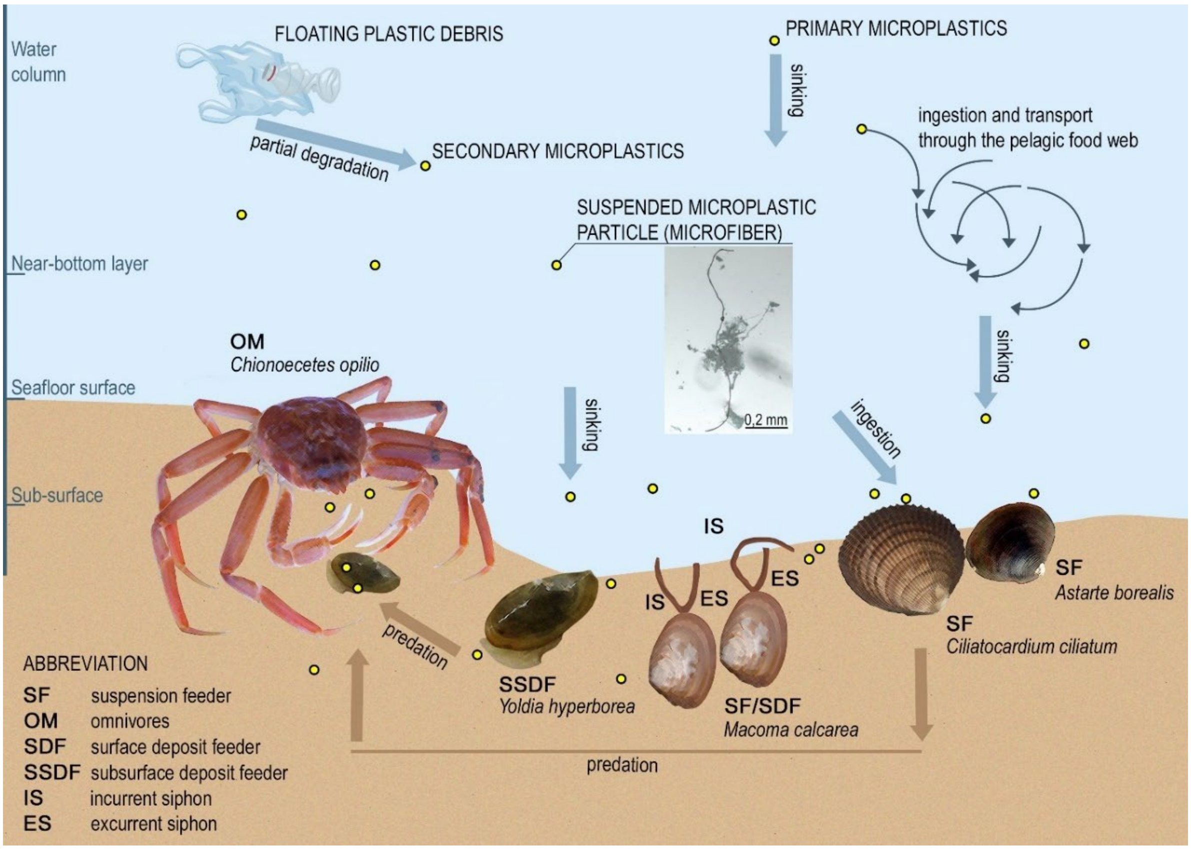


Fig. 4.5 - 1. Conceptual diagram of microplastic ingestion by benthic fauna from different feeding guilds in the Pechora Sea.

The diagram illustrates how suspension- and deposit-feeding bivalve molluscs (*Y. hyperborea*, *M. calcarea*, *C. ciliatum*, *A. borealis*) that dominate macrobenthic assemblages in the Pechora Sea ingest sinking microplastics from the water column and sediments, whereas mobile omnivores (represented by *C. opilio*) ingest microplastics both from the sediments, but also passively from their prey. Figure 4.5 - 1 also shows flexibility in feeding strategies amongst regional biota, with *M. calcarea* being able to adjust position of its siphon and switch from deposit feeding (predominant strategy) to suspension feeding. All species represented in the model (*C. opilio*, *Y. hyperborea*, *M. calcarea*, *C. ciliatum*, *A. borealis*) have been selected based on the outcomes of the current study, with frequencies of microplastic occurrence described for these species in Figure 4.4-2 and feeding behaviour explained in Introduction (Section 4.2.2).

A. borealis–*M. calcarea* have been shown to dominate macrobenthos near Dolgy Island (Denisenko et al., 2019). Near Vaigach Island, macrobenthos form a more heterogeneous community, overall dominated by *A. borealis* – *C. ciliatum* (see Chapter 2). The apex benthic predators in the Pechora Sea include the Atlantic walrus and the common eider duck; no published evidence of microplastics ingestion for these species was evident in the literature. However, the presence of microplastics has been previously recorded in the Arctic and north Atlantic for marine birds, for example northern fulmars (Trevail et al., 2015) and marine mammals including fin whales (Sadove and Morreale, 1989) and bowhead whales (Finley, 2001), it is therefore likely that lack of data on microplastic ingestion by walruses and eiders is due to lack of research rather than absence of microplastics from the food webs in the Pechora Sea.

The present model illustrates significant role of seafloor ecosystems and specifically benthic fauna in accumulating sinking microplastics. It can also be used to demonstrate diversity of feeding strategies of benthic organisms and therefore importance of targeting species from different feeding guilds for monitoring of microplastic accumulation and distribution.

4.5.3. Further research questions

Growing evidence of the presence of microplastics in the Arctic leads to an increasing number of research questions that need to be considered for better understanding of the extent and demonstratable impacts of microplastic contamination. Data collection is a first step towards mitigation of plastic pollution, and at this stage developing, harmonising and adopting international protocols for both pelagic and benthic plastics assessments on a regional scale is crucial to obtaining comparable and reliable data (Kershaw et al., 2019; PAME, 2021).

The high levels of microplastic contamination in *C. opilio* revealed by this study offer concerning insights into plastics accumulation in mobile benthic omnivores, which highlight the need for further investigation of the drivers of accumulation and its ecological consequences. Regular surveys of microplastic contamination are needed in each of the commercial benthic invertebrate species in the Barents Sea, namely *P. camtschaticus*, *C. opilio* and *C. islandica.* Future studies could investigate the physiological mechanisms of plastic ingestion and incorporation of particles into tissues by different organisms and feeding guilds in more detail and determine the timescales over which ingested particles remain in organisms.

In addition to quantitative assessment, chemical characterisation of microplastics, using Fourier transform infrared spectroscopy, Raman spectroscopy, or energy dispersive X-ray spectroscopy, is needed for understanding potential sources of contamination. Advantages and disadvantages of each method are discussed in the GESAMP report (Kershaw et al., 2019) and should be considered on a case-by-case basis, depending on the number and size of particles, budget and timeframes of the project.

For the Arctic Ocean, oceanographic features such as the seasonality of sea ice cover, primary production and riverine discharge need to be considered for effective and representative monitoring (PAME, 2021). In particular, the role of riverine inflow is crucial for understanding the distribution and accumulation of microplastics in the Arctic (Yakushev et al., 2021). Study of the delivery and fate of river-borne plastic litter in the Arctic Ocean requires an end-to-end system-scale understanding of its inflow with fluvial water, transformation in the estuarine and deltaic zones, transport by river plumes during ice-free periods and by sea ice during cold periods, settling to subjacent seawater below river plumes and accumulation at the seafloor. Collection of specific *in situ* data is essential to quantify these processes and determine the key factors that govern the dynamics and variability of transport and accumulation of marine plastic litter in the Arctic Ocean.

Incorporating the following research objectives into the agendas of regional and international programmes focused on microplastic studies in the Arctic, such as the Implementation Plan for the Regional Action Plan on Marine Litter in the Arctic by PAME would help to address the key knowledge gaps in microplastic pollution in the Arctic:

1. Understanding the role and distribution of river-borne versus ice-borne microplastics in the marine environment.
2. Revealing the role of riverine plumes in governing the distribution of microplastics on the pan-Arctic scale.
3. Defining ecotoxicological consequences of microplastic ingestion by commercially valuable species as well as by humans.
4. Investigating differences in physiological mechanisms of microplastic ingestion and inter-tissue translocation by fauna from different feeding guilds.
5. Identifying target species representative of Arctic benthic assemblages, habitats and feeding guilds for monitoring of microplastics ingestion.

4.6. Recommendations for ecological monitoring

Currently plastic litter is considered under SDG 14.1, with the density of floating plastic litter listed among key indicators of ocean pollution (Indicator 14.1.1). However, no other parameters of plastic and microplastic contamination are considered. The present study of microplastic ingestion by benthic fauna in the Arctic agrees with previous studies of microplastic ingestion and contributes to the evidence base for microplastic accumulation in seafloor ecosystems. Macrobenthic communities are suitable for ecological monitoring because of their tendency to accumulate pollutants enables them to demonstrate retrospectively the condition of the marine environment. Changes in macrobenthic community structure are commonly used to detect and monitor impacts of polluting discharges on the marine environment (Henderson and Ross, 1995). Therefore, parameters such as the abundance of microplastic items in seafloor sediments and ingestion rates of microplastics by benthic fauna should be added to the SDG 14 (UNSDG, 2020) as globally-important indicators of plastic pollution. An increasing amount of scientific evidence (e.g., Bergmann et al., 2017b; Fang et al., 2018; Kane et al., 2020; Sfriso et al., 2020; Yakushev et al., 2021) is revealing the global scale of distribution of marine microplastic contamination, including in the polar regions and the deep-sea. International collaboration with global inclusion is needed to address this problem by developing mitigation strategies on a global scale (such as the SDG targets, GESAMP reports and the PWP action plan of the Basel Convention) and implementing action plans on a regional scale (such as those of the AMAP and PAME working groups of the Arctic Council). To summarise, the key recommendation for long-term ecological monitoring of microplastic accumulation in benthic ecosystems of the Pechora Sea based on the outcomes of this chapter is as follows:

It is here suggested that ingestion of microplastics by macrobenthos is added to the SDG14 as a globally-important **indicator of plastic pollution**. In the Arctic region monitoring of microplastics in seawater, sediments and biota, including ingestion levels in macrobenthic invertebrates, should be included in long-term ecosystem monitoring programmes.

- Target species in the Barents Sea ecoregion: commercially harvested species (*P. camtschaticus*, *C. opilio* and *C. islandica),* and species representative of different feeding strategies (suspension feeders (filter feeders and passive suspension feeders), deposit feeders, grazers, predators, omnivores).
- Recommended methods: as per latest guidelines (Kershaw et al., 2019). Chemical characterisation of particles (FTIR or similar) is essential to verify types of plastics.

4.7. Summary

Despite growing evidence of the magnitude of microplastic contamination in the Arctic, sources of plastic pollution and ecological repercussions of ingested microplastics by marine biota are poorly studied and potential harm to human health from ingestion of microplastics is yet to be determined. The present study investigates microplastic ingestion by macrobenthos in the Pechora Sea and its variation.

Ingestion of microplastics by benthic fauna in the Pechora Sea occurs commonly with an average of 29% of stomachs in all macrobenthos containing microplastics. Furthermore, average occurrence of microplastics in 2017–2018 was significantly higher than in 2008, with proven statistical significance of this difference. A conceptual diagram of microplastic accumulation in benthic ecosystems of the Pechora Sea is presented (Figure 4.5-1).

Most of the studied species had ingested microplastics, but occurrence of ingestion varied greatly between the species and feeding guilds. No relationships were found between occurrence of microplastic and size/weight or feeding mode of species. It was also shown that larger sampling sizes allows better detection of microplastic accumulation.

Among the mobile benthic omnivores, the snow crab *Chionoecetes opilio* had the highest rate of occurrence of ingested microplastics. *C. opilio* is an important commercial species in the Russian sector of the Barents Sea with an ongoing fishery since 2016. Therefore, the discovery of ingested microplastics in 35% of *C. opilio* in the Pechora Sea suggests strong potential for the passive consumption of microplastics by humans from seafood.

Finally, it was demonstrated that microplastic ingestion by benthic fauna commonly occurs in the Arctic and is also present in the Kara Sea, Laptev Sea and East-Siberian Seas. However, larger sampling sizes are needed to analyse the spatial distribution of microplastic contamination in the Arctic.

In the Arctic region, a harmonised monitoring program is needed for monitoring microplastic pollution with consideration of regional specificities such as seasonality of the ice cover, primary production and riverine discharge. This study demonstrates high occurrence of ingested microplastics in Arctic benthic fauna and it is recommended to include microplastic ingestion by macrobenthos to the SDG 14 as globally-important indicators of plastic pollution. In the Barents Sea it is of great importance to investigate in more detail ingestion, accumulation and potential translocation of microplastics in commercially exploited invertebrate species *P. camtschaticus*, *C. opilio* and *C. islandica.*

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Chapter 5. Synthesis, conclusions and monitoring recommendations

The concluding chapter of this thesis summarises key findings of the three data chapters, reviews key drivers of environmental change with an impact on benthic ecosystems of the Pechora Sea, and provides future research questions and recommendations for monitoring of the state and dynamics of biodiversity of Arctic benthic ecosystems.

5.1. Key findings

This section summarises key findings of the three core data chapters of this thesis, with an aim to assess the status, variability and biodiversity conservation issues of Arctic benthic ecosystems of the Pechora Sea for improved management.

5.1.1. State and temporal variability of macrobenthos in the Pechora Sea

The key outcomes of this study related to assessment of the present state and variability of macrobenthic communities in the Pechora Sea are as follows:

1) A historical review of benthic research in the Pechora Sea was conducted, literature available from 1920s to 2020 was reviewed (Section 1.3; Appendix 0-1), sampling sites have been consolidated and mapped where possible (Figure 1.3-1). In addition, publicly available outcomes of ecological monitoring carried out at the oil and gas exploration areas in the Pechora Sea have been reviewed (Section 1.3-2).
2) Knowledge gaps in benthic research in the Pechora Sea have been identified, including (1) lack of data from continental shallows and estuaries; (2) lack of time-series data, including long-term observations; (3) inconsistency in methods of data collection and interpretation.
3) New data have been produced to characterise shallow water communities of the Pechora Bay and macrobenthic foraging resources of walruses near Vaigach Island. A data set was developed comprising 345 taxa of benthic invertebrates and six years of observations. Raw abundance and biomass data are available in Appendix 2-6.
4) In the Pechora Bay a monodominant community of *Limecola balthica* with low biomass and low species richness has been described at the margins of its distribution (Section 2.4-1).

5) A highly heterogeneous macrobenthic community overall dominated by an *Astarte borealis-Ciliatocardium ciliatum* assemblage is described near Vaigach Island (Figure 2.4-6), and community structure is analysed in detail in Section 2.4-2. No clear trends were observed for biomass, abundance, production and species composition data in 2015–2020 (Section 2.4-3), however, pairwise comparison revealed differences in biomass in 2015 compared to other years (Table 2.4-5). Year and location of sampling contributed most to variation in macrobenthos (Appendix 2-2).

6) The communities of macrobenthos studied were comprised of Arctic, boreal-Arctic and species with widespread distributions; no signs of borealization of fauna were observed (Table 2.4-10).

7) A need for systematic long-term monitoring to improve understanding of temporal change of macrobenthos has been identified and specific recommendations for ecological monitoring are consolidated below in Section 5.2.

5.1.2. Trophic niche and population dynamics of *Chionoecetes opilio* in the Pechora Sea

In Chapter 3, occurrence, diet and trophic niche of the non-indigenous invasive benthic omnivore, the snow crab *Chionoecetes opilio* were assessed and compared to occurrences and diets of native benthic decapods. The following results have been achieved:

1) Analysis of video recordings obtained in 2016 and in 2020 showed presence of *C. opilio* in the research area near Vaigach Island. Larger and more robust data collection is needed to monitor any change in status of *C. opilio*.

2) None of the male *C. opilio* in the research area reached maturity according to the discriminant morphometric function (Appendix 3-2), suggesting that the Pechora Sea could have a role as a nursery ground for this species, similar to the nearby fjords of the Novaya Zemlya islands (Zalota et al., 2019).

3) Twenty categories of prey items were identified in stomach contents of *C. opilio*, *H. araneus* and *P. pubescens* (Figure 3.4-3).

4) Pianka's overlap measure (following Krebs, 1998) demonstrated overlap in the diets of the three crab species (Section 3.5-2) suggesting that *C. opilio* is competing over foraging resources with *H. araneus* and *P. pubescens*.

5) Among the inclusions in the food lumps, microplastic particles were registered in stomachs of all three species with 28% average occurrence. This is analysed and compared with microplastic occurrence in other benthic organisms in Chapter 4.

6) A conceptual diagram of trophic interspecies relationships between benthic predators and macrobenthic communities in the Pechora Sea was developed (Figure 3.5-3). The present study demonstrates direct trophic competition between *C. opilio* and native benthic decapods, however the trophic relationship between the Atlantic walrus and the snow crab remains uncertain and requires further research.

7) Recommendations for further monitoring of mobile benthic megafauna and specific studies to resolve benthic food web of the Pechora Sea have been suggested and consolidated into overall ecological monitoring recommendations (Section 5.2).

5.1.3. Microplastic accumulation in benthic ecosystems of the Pechora Sea

In Chapter 4, occurrence of a new emerging pollutant in the Arctic region – microplastic fibres – was assessed in stomachs of macrobenthos across different species, feeding guilds and locations in the Pechora Sea and compared to other seas of the Eurasian Arctic. The chapter provides first evidence of microplastic ingestion by macrobenthos in the Pechora Sea; furthermore, temporal variability of microplastic accumulation in the Pechora Sea over the 10-year period was assessed and the following results have been achieved:

1) Ingestion of microplastics by benthic fauna in the Pechora Sea occurs commonly with an average of 29% of stomachs in all macrobenthos containing microplastics. All of the studied species had ingested microplastics (Table 4.4-1), but no relationship was found between occurrence of microplastic and size/weight or feeding mode of species.

2) Average occurrence of microplastics in 2017–2018 was significantly higher than in 2008 (ANOSIM R=0.46; p=0.008, Chi-squared test p=0.0006; Section 4.4.7).

3) It was demonstrated that microplastic ingestion by benthic fauna commonly occurs in the Arctic and is also present in the Kara Sea, Laptev Sea and East-Siberian Seas with an average of 27±6% of stomachs in all macrobenthos containing microplastics. However, larger sampling sizes are needed to support comprehensive analysis of the spatial distribution of microplastic contamination in the Arctic.

4) As 35% of study snow crabs had ingested microplastics in the Pechora Sea, I think this

suggests potential passive consumption of microplastics by humans from seafood.

5) A conceptual diagram of microplastic accumulation in benthic ecosystems of the Pechora Sea was developed (Figure 4.5-1). The diagram illustrates the significant role of macrobenthic communities in accumulation of sinking marine microplastics and the diversity of feeding strategies of benthic organisms leading to different pathways of microplastic ingestion.
6) Further research questions have been identified to tackle key knowledge gaps in microplastic pollution in the Arctic (Section 4.5.3).
7) Recommendations for ecological monitoring in the Pechora Sea have been provided (Section 5.2) and more broadly it is recommended that the ingestion rates of microplastics by benthic fauna should be added to the SDG 14 as globally-important indicators of plastic pollution and its impacts.

5.2. Broader implications and ways forward

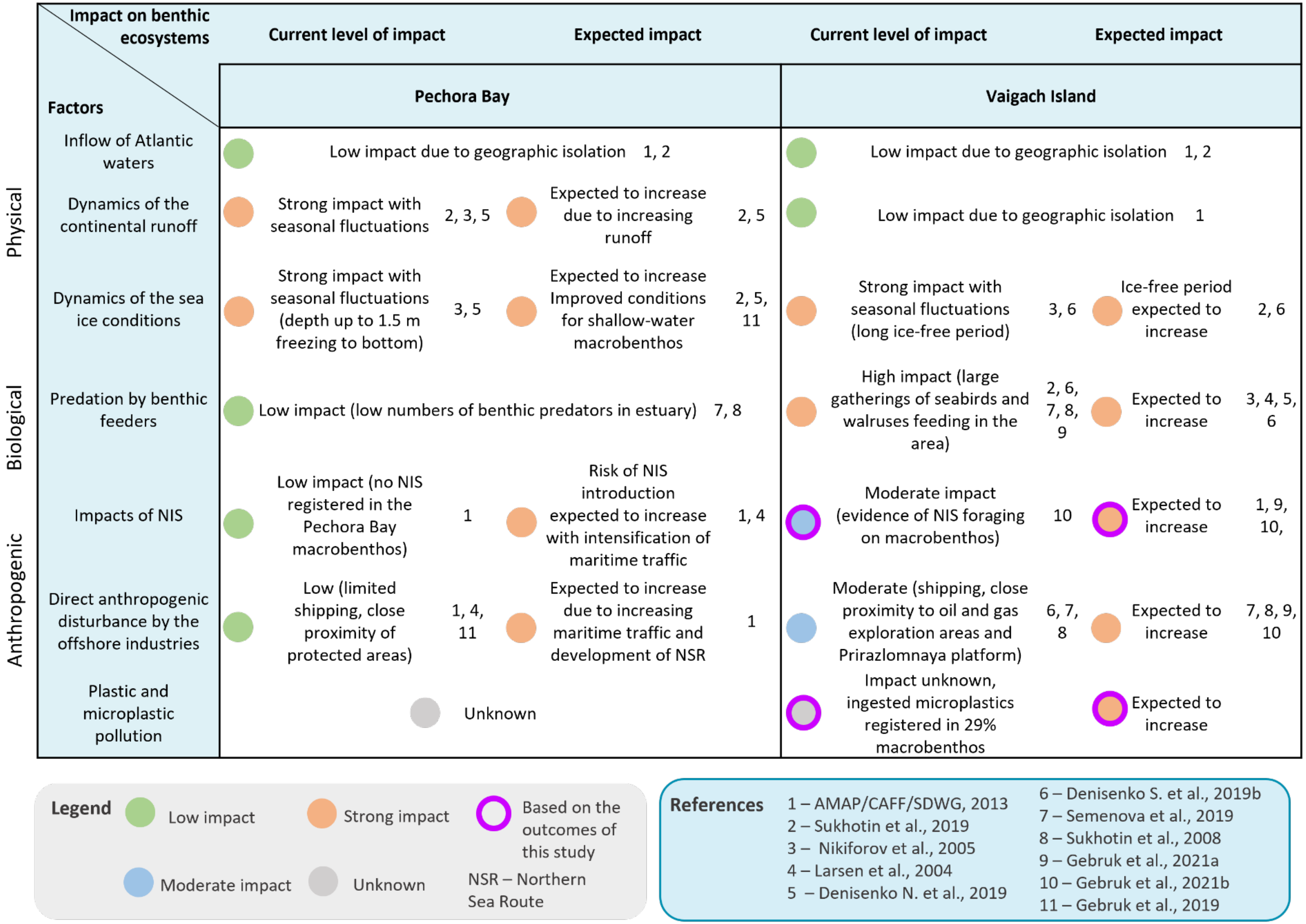
5.2.1. Key stressors of benthic biodiversity in the Pechora Sea

Key physical and anthropogenic drivers of environmental change in the Arctic and their effects on marine ecosystems are reviewed in section 1.1.2. Identified stressors have individual and cumulative impacts on biodiversity in the Arctic Ocean, but their relative importance and scale of impact depend on regional conditions (CAFF, 2017). WWF identified major environmental stressors for the entire Barents Sea ecoregion (Larsen et al., 2004), however no previous attempts have been found in literature to further narrow this list down to the Pechora Sea specifically, which has been listed as an area of heightened ecological significance by the Arctic Council (AMAP/CAFF/SDWG, 2013). Based on the literature review of regional oceanographic conditions, biodiversity, conservation status and socio-economic context (Section 1.2) and observed stressors in benthic ecosystems of the Pechora Sea as the outcomes of this study (Section 5.1), e.g., predation by the omnivorous benthic NIS *C. opilio* and growing plastic pollution, the following parameters can be highlighted as factors with a potential impact on benthic ecosystems of the Pechora Sea:

- Environmental conditions including:
    - Inflow of Atlantic waters;
    - Dynamics of continental run-off through the Pechora River;

    - Sea ice conditions (sea-ice extent and thickness).
- Biological interactions including:
    - Predation by benthic feeders with an additional stressor from an introduced benthic omnivore species the snow crab *C. opilio.*
- Anthropogenic disturbance including:
    - Direct disturbance by the offshore industries including maritime traffic and oil and gas exploration;
    - Pollution (including plastic and microplastic pollution).

Even within the Pechora Sea the level of impact of these factors on macrobenthic communities likely vary in the two research areas, due to the site-specific conditions (e.g., proximity to riverine inflow, abundance of benthic predators, proximity to oil platform). Figure 5.2-1 provides a generic model characterising the observed and expected levels of impact from the key physical, biological and anthropogenic factors on the state of macrobenthic communities in the Pechora Bay and near Vaigach Island. Levels of impact are broadly divided into low, moderate, strong, and unknown (no data available on the level of impact in the Pechora Sea), depending on whether any evidence of impact were found or predicted in the literature or as a result of this study. “Expected impact” is explained as the relative level of impact (strong, moderate, low, or unknown) forecasted in the research areas by 2030 following the Arctic warming trend according to the current climate change projections (AR5, IPCC, 2014; AR6, IPCC, 2021). It is important to highlight that nutrient availability, primary production and persistent pollutants including persistent organic pollutants and toxic metals might also have an impact on benthic ecosystems (Larsen et al., 2004), but have not been assessed in this study. The model illustrates how the outcomes of the present study advance our understanding of ecosystem functioning in the Pechora Sea – purple circles in Figure 5.2-1 indicate where the presence of the stressor is evidenced by this thesis.



	Impact on benthic ecosystems Factors	Current level of impact		Expected impact		Current level of impact		Expected impact	
		Pechora Bay				Vaigach Island			
Physical	Inflow of Atlantic waters	🟢 Low impact due to geographic isolation	1, 2			🟢 Low impact due to geographic isolation	1, 2		
	Dynamics of the continental runoff	🟠 Strong impact with seasonal fluctuations	2, 3, 5	🟠 Expected to increase due to increasing runoff	2, 5	🟢 Low impact due to geographic isolation	1		
	Dynamics of the sea ice conditions	🟠 Strong impact with seasonal fluctuations (depth up to 1.5 m freezing to bottom)	3, 5	🟠 Expected to increase Improved conditions for shallow-water macrobenthos	2, 5, 11	🟠 Strong impact with seasonal fluctuations (long ice-free period)	3, 6	🟠 Ice-free period expected to increase	2, 6
Biological	Predation by benthic feeders	🟢 Low impact (low numbers of benthic predators in estuary)	7, 8			🟠 High impact (large gatherings of seabirds and walruses feeding in the area)	2, 6, 7, 8, 9	🟠 Expected to increase	3, 4, 5, 6
Anthropogenic	Impacts of NIS	🟢 Low impact (no NIS registered in the Pechora Bay macrobenthos)	1	🟠 Risk of NIS introduction expected to increase with intensification of maritime traffic	1, 4	⭕🔵 Moderate impact (evidence of NIS foraging on macrobenthos)	10	⭕🟠 Expected to increase	1, 9, 10,
	Direct anthropogenic disturbance by the offshore industries	🟢 Low (limited shipping, close proximity of protected areas)	1, 4, 11	🟠 Expected to increase due to increasing maritime traffic and development of NSR	1	🔵 Moderate (shipping, close proximity to oil and gas exploration areas and Prirazlomnaya platform)	6, 7, 8	🟠 Expected to increase	7, 8, 9, 10
	Plastic and microplastic pollution	⚪ Unknown				⭕⚪ Impact unknown, ingested microplastics registered in 29% macrobenthos		⭕🟠 Expected to increase	

Legend
🟢 Low impact
🟠 Strong impact
⭕ Based on the outcomes of this study
🔵 Moderate impact
⚪ Unknown
NSR – Northern Sea Route

References
1 – AMAP/CAFF/SDWG, 2013
2 – Sukhotin et al., 2019
3 – Nikiforov et al., 2005
4 – Larsen et al., 2004
5 – Denisenko N. et al., 2019
6 – Denisenko S. et al., 2019b
7 – Semenova et al., 2019
8 – Sukhotin et al., 2008
9 – Gebruk et al., 2021a
10 – Gebruk et al., 2021b
11 – Gebruk et al., 2019

Fig. 5.2 - 1. Observed and expected levels of impacts of key drivers of environmental change on benthic ecosystems of the Pechora Sea based on literature review and outcomes of this thesis.

Both research areas are geographically isolated from ocean currents of Atlantic origin (Figure 1.2-2) and therefore are less influenced by the temperature rise related to inflow of the Atlantic water mass. Reduction in sea ice volume alongside increased riverine input can improve conditions for growth of *L. balthica* and other shallow-water eurythermal and euryhaline species in Pechora Bay; however, time series data are needed to detect impacts of the dynamics of hydrography on macrobenthos. Bivalve communities near Vaigach Island that are heterogeneous, diverse and rich in biomass did not show evidence of an overall change during the six years of observations in this study (Section 2.5.3). However, the dynamics of the climatic index in the Barents Sea (Boitsov et al., 2012) suggest that the period of temperature fluctuations can be approximated as 25–35 years, such that long-term observations are needed to observe response to these trends in macrobenthic communities. Long-term cumulative impacts of changing environmental conditions, introduction of non-indigenous species (including the invasive benthic omnivore, the snow crab *C. opilio*) and anthropogenic disturbance including plastic pollution remain uncertain and require further systematic monitoring. Recommended approaches to ecological monitoring, including the parameters to measure, are provided below in Section 5.2.2.

5.2.2. Recommendations for ecological monitoring in the Pechora Sea

A standardised approach to data collection and management with compatible standards and procedures for analyses and data sharing is essential for successful implementation of ecosystem-based management in the Arctic (CAFF, 2017). Whilst some regional-scale observation systems have begun to appear in the Arctic, such as the Svalbard Integrated Earth Observing System (SIOS) or the Sustaining Arctic Observing Networks (SAON) initiative, there is still a clear lack of an internationally recognised coordinated Arctic observing framework that has been identified by numerous reports of the Arctic Council (Gill et al., 2011; CAFF, 2013; CAFF, 2017), and addressed in the Arctic stakeholder meetings such as the biennial Arctic Observing Summit (Murray et al., 2018) and the Arctic Science Ministerial (ASM2, 2019).

Long-term ecological monitoring can advance understanding of cumulative impacts of changing environmental conditions and anthropogenic disturbance, help to detect and predict changes in the macrobenthic communities, such as shifts in the communities, species replacement, borealization of fauna and reduction of Arctic species, shifts in the distribution range, and other processes. Specific recommendations are given below, aimed at improving approaches to monitoring of benthic biodiversity in the Pechora Sea.

Macrobenthic communities

To monitor dynamics of macrobenthos in the foraging grounds of the Atlantic walrus near Vaigach Island, it is recommended to continue sampling in the selected research sites following the initial assessment of foraging macrobenthos conducted by the WWF in 2015–2016 (Gebruk et al., 2021a) and continued in the present study (Section 2.4-3). Species composition, abundance and biomass should be recorded to enable coherent community analysis with voucher specimens ground truthed by expert class/order level taxonomists and kept available for multi locus genetics. It is also recommended to consider where possible the addition of dry mass measurement for biomass with a standardised protocol.

Continued monitoring at the five research sites previously sampled in 2015–2020 is recommended for long-term monitoring. The outcomes of this study suggest that the sampling gear, more specifically the volume of the benthic grab, had a negligible effect on variability of macrobenthos (Appendix 2-2). Therefore, a smaller *Okean-0.1* grab or a functional analogue *Van-Veen* bottom grab that are currently used in ecological monitoring in the oil and gas licensed areas (Gasprom, 2018; Shishkin et al., 2020) are suitable for long-term monitoring of macrobenthos in the Pechora Sea. The biomass of key prey items, including *A. borealis*, *C. ciliatum* and *A. montagui*, can be used as an indicator parameter of foraging capacity of the area. No such monitoring efforts are currently carried out in the Pechora Bay, and it is recommended to establish a long-term monitoring programme to understand the state and dynamics of shallow-water estuarine communities.

Mobile benthic megafauna

Video transects and images obtained using underwater cameras and ROVs are recommended to assess abundance of mobile benthic megafauna and monitor the state of population of the non-indigenous benthic predator *C. opilio* near Vaigach Island. Installation of laser scale indicators (minimum two) with a set distance between them provides the size reference essential to assess the size composition of the snow crab population (Zalota et al., 2019). It is recommended to use angled cameras where possible and keeping the speed, direction, lighting and distance from seafloor consistent. For biological analyses including sex composition of population and diet studies, biological samples are needed. It has been demonstrated for the Kara Sea that adult snow crabs are likely underrepresented in the trawl samples (Zalota et al., 2019); it is therefore recommended to combine data from scientific trawls, baited traps and ROV assessments to assess the entire population including different size groups. To resolve the trophic relationship between the snow crab and the Atlantic walrus, molecular genetic analysis is required to trace crab DNA in walrus faecal samples.

Microplastic pollution

A harmonised monitoring programme is needed for monitoring microplastic pollution in the entire Arctic region with consideration of regional specificities such as seasonality of the ice cover, primary production and riverine discharge. It is further recommended to include microplastic ingestion rates of macrobenthos in the SDG 14 as globally-important indicators of plastic pollution. In the Barents Sea ecoregion, it is of great importance to investigate in more detail the ingestion, accumulation and potential translocation of microplastics in commercially exploited invertebrate species, namely the red king crab (*Paralithodes camtschaticus*), the snow crab (*Chionoecetes opilio*) and the Iceland scallop (*Chlamys islandica*). In the Pechora Sea, it is recommended to study microplastic ingestion as a part of long-term monitoring of macrobenthos. Quantitative assessment needs to be verified by chemical characterisation of all identified particles following the latest GESAMP guidelines (Kershaw et al., 2019). It is recommended to use FTIR to identify all potential microplastics as well as developing more robust methods for establishing non airborne contamination.

Figure 5.2-2 provides a short summary of the key recommendations including monitoring parameters and techniques, integration of which into the regional ecological monitoring programmes could lead to a more coherent understanding of the state and dynamics of the Pechora Sea benthic ecosystems. Each block of recommendations consists of a larger scale overarching approach that can be implemented for ecological monitoring in all Arctic seas, followed by specific recommendations developed for monitoring of benthic biodiversity in the Pechora Sea.

Integrated approach to long-term ecological monitoring of the Pechora Sea benthic ecosystems

1. To understand dynamics and cumulative impacts of stressors on Arctic benthic biodiversity, **long term monitoring** of macrobenthic communities is required. **Standardised framework of data collection** specifying number and locations of sampling sites, sampling gear, analysed parameters and target species is essential to ensure data compatibility.

- Time series comprising minimum of 25-years of data collection is required to assess dynamics of macrobenthos against the dynamics of climatic index of the Barents Sea.
- Standardised protocol for biomass measurement is essential, it is recommended to include wet mass, dry mass and ash-free dry mass.
- A spatially nested design of sampling sites should be considered.
- Voucher specimens should be kept for more robust cross checking, and preservation suitable for multi locus genetic studies.
- Additional environmental data collected should include CTD casts for the water column and primary production measurements.
- Toxicology tests are recommended for key prey items.
- Specific recommendations for Vaigach Island research area: (1) sample size - minimum 5 sites, (2) sampling gear – benthic grab with a 0.1 m^2 sample area with a minimum of 3 replicates each; (3) biomass of *A. borealis*, *C. ciliatum* and A. *montagui* can be used as an indicator of foraging capacity of walruses. For indicator species, it is also recommended to include morphometric indices and reproductive status monitoring for population assessment.

2. Combination of data from **multiple sources** needed to assure complex assessment of benthic ecosystems including **mobile megafauna**.

- Combination of scientific trawls, baited traps and ROV assessments is recommended to assess full scope data for different size groups.
- ROV video observations are recommended for assessment of mobile megafauna in the Pechora Sea. Parallel laser pointers spaced at a known angle and distance apart (laser scale) are recommended to provide size reference. Keeping the speed, direction, lighting and distance from seafloor consistent can improve the quality (and quantity) of data.
- To resolve trophic relationship between the snow crab and the Atlantic walrus, molecular genetic analyses is needed to trace the crab DNA in walrus faecal samples.

3. It is here suggested that **ingestion of microplastics by macrobenthos** is added to the SDG14 as a globally-important indicator of plastic pollution. In the Arctic region monitoring of microplastics in seawater, sediments and biota, including ingestion levels in macrobenthic invertebrates, should be included in long-term ecosystem monitoring programmes.

- Target species in the Barents Sea ecoregion: commercially harvested species (*P. camtschaticus*, *C. opilio* and *C. islandica*), and species representative of different feeding strategies (suspension feeders (filter feeders and passive suspension feeders), deposit feeders, grazers, predators, omnivores).
- Recommended methods: as per latest guidelines (Kershaw et al, 2019). Chemical characterisation of particles (FTIR or similar) is essential to verify types of plastics.

Fig. 5.2 - 2. Infographic of an approach to integrated monitoring of the Pechora Sea benthic ecosystems.

5.2.3. Summary and closing remarks

Long-term ecological monitoring with a consistent framework for data collection and interpretation is required to detect and predict changes in Arctic marine ecosystems in an effective manner, including in benthic biodiversity, and to tackle the knowledge gaps identified in this thesis. These are (1) long-term dynamics of the Pechora Sea macrobenthos in response to changing environmental conditions and anthropogenic disturbance; (2) impacts of the invasive benthic predator *C. opilio* on future benthic biodiversity of the Pechora Sea; (3) ecotoxicological impacts of accumulation of microplastics in benthic ecosystems on marine biodiversity and human health. Recommendations provided in this thesis (Figure 5.2-2) include overarching principles that can also be implemented in other shelf seas of the Arctic Ocean, and region-specific methodological recommendations that can improve existing frameworks of ecological monitoring and biodiversity conservation in the Pechora Sea, such as ecological monitoring programmes currently implemented in the oil and gas exploration licensed areas. This thesis improves the baseline knowledge on biodiversity and state of ecosystems in an ecologically significant area of the Arctic, the Pechora Sea, and provides an important case study illustrating how research outcomes, e.g., demonstration of trophic competition between the non-indigenous *C. opilio* and native benthic predators, and first evidence of microplastic accumulation in benthic organisms in the Pechora Sea, can improve management through advancements in frameworks of ecological monitoring.

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Appendices

Thesis Overview

Appendix 0-1. Overview matrix of all sampling sites studied in this thesis

Year, date of sampling, water depth at the site, site number, coordinates, sampling gear*, and number of repeats are shown for each sampling site. Green shading indicates expeditions were author participated and collected samples personally. Yellow shading indicates expeditions organised by LMSU MRC and sampled by the hydrobiology unit of LMSU MRC. Purple shading indicates historical samples taken from zoological archives of IO RAS.

Year	Site number	Coordinates (DDM)*		Sampling gear**						Sampling date (day, month,	Water depth, m
		N	E	1	2	*3*	4	5	6		
2008 – RV *Ivan Petrov*, Pechora Sea (expedition organised by IO RAS)											
2008	1	69°37.041'	56°4.317'	3	-	-	-	-	-	12.11.2008	38
2008	2	69°35.441'	56°4.728'	3	-	-	-	-	-	11.11.2008	38
2008	3	69°37.744'	56°6.474'	3	-	-	-	-	-	11.11.2008	36
2008	4	69°35.343'	56°3.111'	3	-	-	-	-	-	12.11.2008	39
2008	7	69°36.513'	56°1.661'	3	-	-	-	-	-	12.11.2008	38
2008	8	69°36.280'	56°0.506'	3	-	-	-	-	-	11.11.2008	39
2008	9	69°35.969'	56°0.200'	3	-	-	-	-	-	11.11.2008	39
2008	11	69°35.436'	56°1.879'	3	-	-	-	-	-	12.11.2008	39
2008	12	69°35.565'	56°2.935'	3	-	-	-	-	-	12.11.2008	38.5
2008	13	69°36.076'	56°3.428'	3	-	-	-	-	-	12.11.2008	39
2008	15	69°36.215'	56°1.632'	3	-	-	-	-	-	11.11.2008	39
2008	17	69°35.911'	56°0.762'	3	-	-	-	-	-	11.11.2008	38.5
2008	19=4	69°35.343'	56°3.111'	3	-	-	-	-	-	11.11.2008	39
2008	21=3	69°37.744'	56°6.474'	3	-	-	-	-	-	11.11.2008	36
2008	23=1	69°37.041'	56°4.317'	3	-	-	-	-	-	11.11.2008	38
2015 – RV *Kartesh*, Vaigach Island (expedition organised by LMSU MRC)											
2015	2015_1	69° 21.137'	58° 56.972'	3	-	-	-	-	-	03.07.2015	22.5
2015	2015_2	69° 36.562'	59° 42.861'	3	-	-	-	-	-	03.07.2015	25.77
2015	2015_3	69° 42.725'	58° 0.507'	3	-	-	-	-	-	03.07.2015	25.35
2015	2015_4	69° 54.477'	58° 29.998'	3	-	-	-	-	-	05.07.2015	25.25
2015	2015_5	69° 36.682'	58° 29.431'	3	-	-	-	-	-	05.07.2015	29.18
2015	2015_6	69° 37.940'	58° 55.533'	3	-	-	-	-	-	05.07.2015	25.87
2015	2015_7	69° 36.064'	58° 7.031'	3	-	-	-	-	-	05.07.2015	18.32
2015	2015_8	69° 45.498'	58° 55.377'	3	-	-	-	-	-	05.07.2015	10.82
2015	2015_9	69° 23.527'	59° 16.807'	3	-	-	-	-	-	05.07.2015	18.4
2015	2015_10	69° 44.983'	58° 29.136'	3	-	-	-	-	-	09.07.2015	30.4
2015	2015_11	69° 26.114'	58° 10.276'	3	-	-	-	-	-	09.07.2015	25.2
2015	2015_12	69° 37.535'	58° 40.143'	3	-	-	-	-	-	09.07.2015	30
2015	2015_13	69° 28.708'	58° 42.804'	3	-	-	-	-	-	09.07.2015	35.18
2015	2015_14	69° 21.137'	58° 56.972'	3	-	-	-	-	-	09.07.2015	33.22
2016 – Pechora Bay (expedition organised by LMSU MRC)											
2016	2016_PeB	68°53.521'	53°38.039'	-	-	-	-	3	-	25.08.2016	1.6
2016	2016_PeB	68°53.463'	53°39.344'	-	-	-	-	3	-	25.08.2016	1.1
2016	2016_PeB	68°53.485'	53°41.441'	-	-	-	-	3	-	25.08.2016	1.3
2016	2016_PeB	68°53.557'	53°44.139'	-	-	-	-	3	-	26.08.2016	1.2
2016	2016_PeB	68°54.191'	53°45.196'	-	-	-	-	3	-	30.08.2016	1.1
2016	2016_PeB	68°54.573'	53°46.585'	-	-	-	-	3	-	30.08.2016	1.4
2016	2016_PeB	68°55.138'	53°47.575'	-	-	-	-	3	-	30.08.2016	1.2
2016	2016_PeB	68°54.520'	53°49.128'	-	-	-	-	3	-	30.08.2016	1.8

Year	Site number	Coordinates (DDM)*		Sampling gear**						Sampling date (day, month,	Water depth, m
		N	E	1	2	*3*	4	5	6		
2016 – RV *Kartesh*, Vaigach Island (expedition organised by LMSU MRC)											
2016	2016_1	69°27.180'	58°33.651'	1	1	-	1	-	-	09.07.2016	9
2016	2016_4	69°36.411'	58°29.422'	3	1	-	-	-	-	09.07.2016	23
2016	2016_6	69°26.734'	58°09.816'	3	1	-	1	-	-	09.07.2016	30
2016	2016_10	69°36.436'	58°06.222'	3	1	-	1	-	-	09.07.2016	26
2016	2016_11	69°37.565'	58°55.394'	3	1	-	1	-	-	09.07.2016	25
2016	2016_1w	69°35.115'	58°31.242'	3	1	-	1	-	-	09.07.2016	25
2016	2016_11	69°31.553'	58°08.465'	3	1	-	-	-	-	09.07.2016	28
2016	2016_1N	69°43.718'	59°25.786'	3	1	-	1	-	-	10.07.2016	25
2016	2016_2N	69°42.509'	59°05.248'	2	1	-	-	-	-	10.07.2016	25
2016	2016_3N	69°42.259'	58°46.335'	-	3	-	1	-	-	10.07.2016	26
2016	2016_4N	69°45.635'	58°57.347'	3	1	-	1	-	-	10.07.2016	28
2016	2016_5N	69°48.155'	59°08.034'	3	1	-	-	-	-	10.07.2016	30
2016	2016_6N	69°48.642'	58°54.716'	1	-	-	1	-	-	10.07.2016	41
2016	2016_7N	69°47.342'	58°44.148'	-	1	-	-	-	-	11.07.2016	27
2016	2016_8N	69°49.034'	58°27.683'	1	3	-	1	-	-	10.07.2016	40
2016	2016_9N	69°50.727'	58°45.804'	-	3	-	1	-	-	10.07.2016	39
2016	2016_10	69°51.818'	58°54.302'	1	2	-	1	-	-	11.07.2016	29
2016	2016_11	69°55.629'	58°41.640'	1	3	-	1	-	-	11.07.2016	32
2016	2016_11	69°56.821'	58°44.182'	-	2	-	1	-	-	11.07.2016	66
2016	2016_12	69°54.413'	58°30.867'	1	2	-	1	-	-	11.07.2016	44
2017 – RV *Kartesh*, Vaigach Island (expedition organised by LMSU MRC)											
2017	2017_4	69°36.411'	58°29.422'	4	4	-	-	-	-	29.07.2017	23
2017	2017_6	69°26.734'	58°09.816'	3	3	-	-	-	-	29.07.2017	30
2017	2017_11	69°31.553'	58°08.465'	3	4	-	-	-	-	30.07.2017	28
2017	2017_1w	69°35.115'	58°31.242'	3	3	-	-	-	-	30.07.2017	25
2017	2017_9N	69°50.727'	58°45.804'	-	-	1	-	-	-	01.08.2017	29
2017	2017_4N	69°45.635'	58°57.347'	-	-	1	-	-	-	01.08.2017	28
2018 – RV *Kartesh*, Vaigach Island (expedition organised by LMSU MRC)											
2018	2018_9N	69°50.727'	58°45.804'	-	3	1	-	-	-	14.07.2018	29
2018	2018_4N	69°45.635'	58°57.347'	-	3	1	-	-	-	15.07.2018	28
2019 – RV *Kartesh*, Vaigach Island (expedition organised by LMSU MRC)											
2019	2019_4	69°36.411'	58°29.422'	3	-	-	-	-	-	07.10.2019	23
2019	2019_6	69°26.734'	58°09.816'	3	-	-	-	-	-	07.10.2019	30
2019	2019_11	69°31.553'	58°08.465'	3	-	-	-	-	-	07.10.2019	28
2019	2019_9N	69°50.727'	58°45.804'	3	-	-	-	-	-	07.10.2019	29
2019	2019_4N	69°45.635'	58°57.347'	3	-	-	-	-	-	07.10.2019	28
2019 – RV *AMK*-78, Eurasian Arctic: the Kara, Laptev, East-Siberian Seas (expedition organised by LMSU											
2019	6490	73°6.503'	130°20.661	-	-	-	-	-	3	06.10.2019	21
2019	6506	75°13.581'	128°38.371	-	-	-	-	-	3	08.10.2019	46
2019	6537	73°34.544'	73°20.177'	-	-	-	-	-	3	17.10.2019	20
2019	6539	73°49.900'	73°14.900'	-	-	-	-	-	3	17.10.2019	30
2019	6473	74°54.268'	160°56.414	-	-	-	-	-	3	01.10.2019	45.5
2020 – RV *Kartesh*, Vaigach Island (expedition organised by LMSU MRC)											
2020	2020_4	69°36.411'	58°29.422'	4	-	-	1	-	-	7.10.2019	23
2020	2020_6	69°26.734'	58°09.816'	4	-	-	1	-	-	7.10.2019	30
2020	2020_11	69°31.553'	58°08.465'	4	-	-	2	-	-	7.10.2019	28
2020	2020_9N	69°50.727'	58°45.804'	4	-	-	2	-	-	7.10.2019	29
2020	2020_4N	69°45.635'	58°57.347'	4	-	-	2	-	-	7.10.2019	28

* Degrees, Decimal Minutes (DDM)

** Sampling gear: 1 – Benthic Grab (Okean-0.1); 2 – Benthic Grab (Okean-50); 3 – Bottom Sigsbee trawl (1.5 m); 4 – ROV Gnom; 5 – Hand shovel (0.05 m^2); 6 – Box-corer (0.5 m^2)

Chapter 1

Appendix 1-1. Synthesis table with expedition details of benthic surveys conducted in the Pechora Sea since 1920s (research vessel, research area, number of sites, sampling gear, depth range, expedition outcomes (published articles), and an institution-organiser are shown for each expedition where specified)

Years of sampling	Research Vessel	Research area	Number of sites	Sampling gear*	Water depth (m)	Outcomes (publications)**	Institution – organiser***
1924 1925	RV *Persey*	Spread across the Pechora Sea	1924– 24 sites 1925 – 14 sites	Benthic grab *Okean-50*	9-185 m	Zenkevich, 1927 Brotskaya and Zenkevich, 1939	IMFO USSR
1958 1959	RV *Professor Derugin*	Spread across the Pechora Sea	1958 – 30 sites 1959 – 34 sites	*Van Veen* benthic grab	(10-200 m approx.)	Galkin, 1964; Galkin, 1998 Denisenko, 2013	MMBI RAS
1970	RV *Nikolay Maslov*	Spread across the Pechora Sea	118 sites	Benthic grab *Okean-50*	(10-200 m approx.)	Antipova, 1973	PINRO
1992 1995	RV *Professor Vladimir Kuznetsov*	Spread across the Pechora Sea	1992 - 18 sites 1995 - 7 sites	*Van Veen* benthic grab	7-210 m	Denisenko et al., 2003 Denisenko, 2013	MMBI RAS, ZIN RAS
1992 1993	RV *Dalnie Zelentsy*	Spread across the Pechora Sea	1992 - 15 sites 1993 – 38 sites	*Van Veen* benthic grab	8-207 m	Dahle et al., 1998 Denisenko et al., 2003	MMBI RAS
1993	Not known	Area of *Prirazlomnoye* oil field	112 sites	Benthic grab, trawl, underwater photography	11-187 m	Pogrebov et al., 1997	RINCAN, VNIIOKEANOLOGIYA
1995	RV *Geophysic*	Pechora Bay	22 sites	*Van Veen* benthic grab	3-18 m	Denisenko et al., 2019b	MMBI RAS
1998	RV *Akademik Sergey Vavilov*	Pechora Bay to Dolgy Island	37 sites	Benthic grab *Okean-0.1*; Benthic grab *Okean-50*; *Sigsbee* trawl	5-28 m	Kucheruk et al., 2003	IO RAS
2003	RV *Professor Shtokman*	Central area of the sea east of Dolgy Island	19 sites	Benthic grab *Okean-50*	16-22 m	Kozlovsky et al., 2019	IO RAS LMSU MRC

Years of sampling	Research Vessel	Research area	Number of sites	Sampling gear*	Water depth (m)	Outcomes (publications)**	Institution – organiser***
2007	RV *Professor Vladimir Kuznetsov*	Dolgy Island	5 quadrats + 3 trawl dredgings + 45 grab samples	Quadrats (0.1 m^2); *Van Veen* benthic grab; *Sigsbee* trawl	0-3 m	Sukhotin et al., 2008	ZIN RAS
2008	RV *Ivan Petrov*	Central Pechora Sea	23 sites	Benthic grab *Okean-0.1*	38-39 m	N/A	IO RAS
2012 2013	RV *Dalnie Zelentsy*	South-eastern Pechora Sea from the Pechora Bay to Dolgy Island	40 sites	*Van Veen* benthic grab	6-72 m	Gerasimova et al., 2019	MMBI RAS, St. Petersburg State University
2014 2016	RV *Professor Vladimir Kuznetsov*	Matveev and Dolgy Islands	2014 – 18 sites 2016 – 6 sites	*Van Veen* benthic grab	10-23 m	Denisenko et al., 2019a	ZIN RAS

**Van-Veen* and *Okean-0.1* benthic grabs have a 0.1 m^2 capture area; *Okean-50*, also known as modified *Petersen's grab* with a 0.25 m^2 capture area

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***IMFO USSR – Institute of marine fisheries and oceanography of the USSR; IO RAS - Shirshov Institute of Oceanology of the Russian Academy of Sciences; LMSU MRC – Lomonosov Moscow State University Marine Research Center; MMBI RAS – Murmansk Marine Biological Institute Russian Academy of Sciences; PINRO - Nikolai M. Knipovich Polar Research Institute of Marine Fisheries and Oceanography; RINCAN - State Research Institute for Nature Conservation of the Arctic and the North; VNIIOKEANGEOLOGIYA - All-Russia Research Institute for Geology and Mineral Resources of the Worm Ocean; ZIN RAS – Zoological Institute of the Russian Academy of Science

Chapter 2

Appendix 2-1. Outcomes of SIMPER analyses for biomass and abundance data (2015-2020)

Biomass (only species with average contribution >1% are shown)

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean 2015	Mean 2016	Mean 2017	Mean 2018	Mean 2019	Mean 2020
Astarte borealis	18.20	21.01	21.01	4.12	37.90	27.70	84.20	37.20	40.30
Serripes groenlandicus	10.36	11.97	32.98	0.26	9.04	35.40	2.16	7.25	40.00
Ciliatocardium ciliatum	9.57	11.05	44.03	0.57	21.20	17.80	4.38	14.20	21.80
Macoma calcarea	6.19	7.15	51.17	10.20	6.36	8.86	5.36	1.47	2.69
Astarte montagui	6.18	7.14	58.31	7.48	9.89	0.81	0.00	0.00	0.00
Astarte crenata	2.96	3.41	61.72	0.00	0.00	8.76	1.47	9.82	5.59
Galathowenia oculata	2.40	2.77	64.49	4.60	0.46	3.82	0.03	0.00	1.13
Pentamera calcigera	2.28	2.64	67.13	0.00	0.00	0.00	38.30	0.00	0.74
Nephtys ciliata	2.16	2.50	72.15	0.80	2.17	2.96	2.20	2.04	1.92
Buccinum scalariforme	2.01	2.33	74.47	4.60	1.35	0.00	0.00	0.00	0.00
Balanus balanus	1.41	1.63	76.10	0.00	0.00	0.00	0.00	18.60	0.03
Yoldia hyperborea	1.08	1.24	77.35	1.15	1.28	1.33	0.69	0.81	1.15

Abundance (only species with average contribution >1% are shown)

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean 2015	Mean 2016	Mean 2017	Mean 2018	Mean 2019	Mean 2020
Galathowenia oculata	11.18	14.79	14.79	299.00	141.00	411.00	2.67	0.00	545.00
Levinsenia gracilis	6.99	9.24	24.03	209.00	26.20	325.00	110.00	183.00	139.00
Maldane sarsi	3.49	4.62	28.65	130.00	32.60	27.20	0.00	26.70	56.00
Flabelligera affinis	3.44	4.56	33.21	0.00	1.48	0.00	0.00	446.00	0.00
Chaetozone setosa	2.98	3.94	37.15	71.70	25.50	99.20	0.00	113.00	123.00
Scoloplos armiger	2.74	3.62	40.77	79.80	37.00	96.20	122.00	0.00	85.00
Macoma calcarea	2.66	3.52	44.29	40.70	47.20	50.80	284.00	49.30	72.00
Protomedeia fasciata	2.45	3.23	47.52	67.10	35.50	10.10	125.00	0.00	2.00
Micronephthys minuta	2.36	3.12	50.64	35.70	15.00	37.00	109.00	88.60	118.00
Ampharete sp.	2.28	3.01	53.65	23.60	1.28	0.00	38.30	0.00	300.00
Ophelina acuminata	1.76	2.32	55.97	1.43	0.43	0.00	0.67	5.33	325.00
Nematoda Gen.sp.	1.29	1.71	57.69	17.90	13.30	86.60	0.00	0.00	0.00
Eteone flava	1.21	1.60	59.29	28.10	13.10	10.40	47.70	42.70	55.00
Diastylis sulcata	1.07	1.41	60.70	47.10	4.92	3.17	0.00	4.67	0.00
Thyasira sarsi	1.05	1.39	62.09	1.19	7.56	46.20	0.00	52.00	48.50
Lysippe labiata	1.03	1.36	63.45	16.20	11.10	28.60	49.80	34.00	36.50

Appendix 2-2. PERMANOVA outcomes for different parameters of sampling

(1) PERMANOVA for Year of sampling (Ye), Sampling site (St), and Sampling gear (Ge)

Design:

Resemblance: D1 Euclidean distance

Number of permutations: 999

Factors

Name	Abbreviation	Type	Levels	Levels explained
Year of sampling	ye	Fixed	5	2015, 2016, 2017, 2018, 2019, 2020
Sampling site	St	Fixed	6	4, 6, 4N, 9N, 1w16, 11w16
Sampling gear	ge	Random	2	Benthic grab Okean – 0.1; Benthic grab Ocean-50

Outcomes:

PERMANOVA table of results

Source	df	SS	MS	Pseudo-F	P (permutations)	Unique permutations
ye	3	2.40E+09	79975	6.75	0.06	909
St	4	4.52E+09	1.13E+09	10.265	0.002	999
ge	0	0		No test		
ye x St**	9	5.98E+09	66408	3.05	0.041	999
ye x ge**	1	9864,4	9864,4	0.45	0.707	995
St x ge**	3	28892	9630,8	0.43	0.817	999
ye x St x ge**	2	39391	19696	0.89	0.359	999
Res	78	1.71E+10	21893			
Total	104	3.65E+10				

Estimates of components of variation.

Source	Estimate	Square root
S (ye)	5630.3	75.035
S (St)	12454	111.6
V (ge)	No test	
S (ye x St)	12434	111.51
V (ye x ge)	-1531.4	-39.133
V (St x ge)	-2898	-53.833
V (ye x St x ge)	-805.51	-28.381
V (Res)	21893	147.96

Conclusion:

Sampling gear (Ge) excluded from further analysis.

(2) PERMANOVA for Year of sampling (Ye) and Sampling site (St)

Design:

Resemblance: D1 Euclidean distance

Number of permutations: 999

Factors

Name	Abbreviation	Type	Levels	Levels explained
Year of sampling	ye	Fixed	5	2015, 2016, 2017, 2018, 2019, 2020
Sampling site	St	Fixed	6	4, 6, 4N, 9N, 1w16, 11w16

Outcomes:

PERMANOVA table of results

Source	df	SS	MS	Pseudo-F	P (permutations)	Unique permutations
ye	4	4.40E+09	1.10E+09	5.23	0.001	999
St	5	5.91E+09	1.18E+08	5.63	0.001	997
ye x St	10	1.02E+10	1.02E+09	4.86	0.001	999
Res	85	1.79E+10	21010			
Total	104	3.65E+10				

Estimates of components of variation

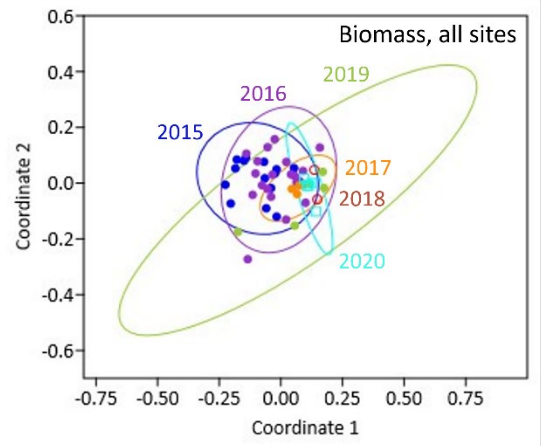
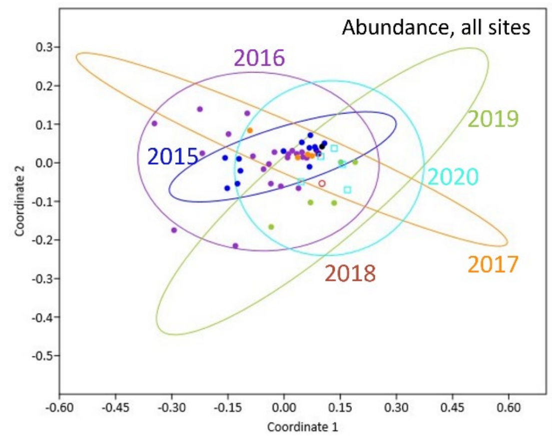
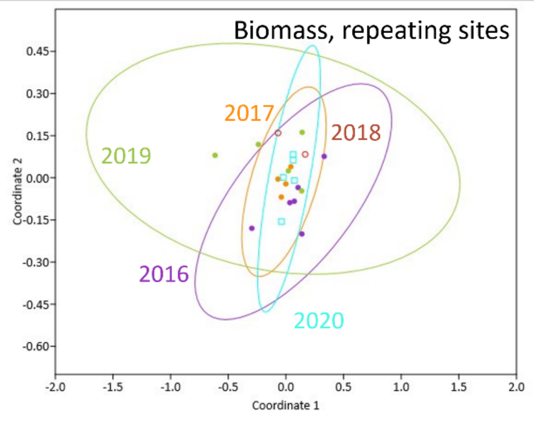
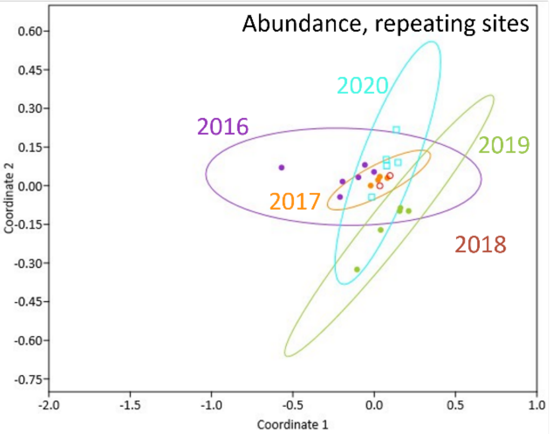
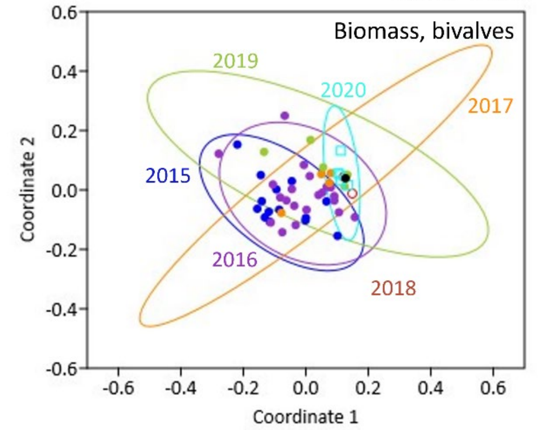
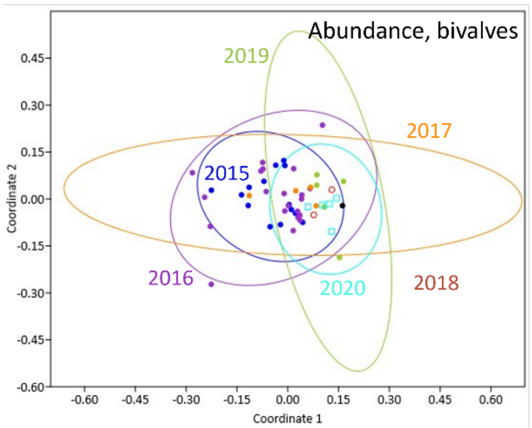
Source	Estimate	Square root
S (ye)	5613.2	74.922
S (St)	7257.2	85.189
S (ye x St)	18006	134.19
V (Res)	21010	144.95

Conclusion:

Combination of the Year of sampling (Ye) and Sampling site (St) has the largest contribution to variation of macrobenthos.

Appendix 2-3. nMDS plots for pooled biomass and abundance data

nMDS plots for biomass and abundance data (for all sites and all species, repeating sites only, bivalves only, and polychaetes only) with 95% confidence ellipses illustrating years of sampling: blue – 2015; violet – 2016; orange – 2017; dark red - 2018; green – 2019; green – 2020.

	Biomass* *relative fractions of each species biomass (g/m^2) to mean biomass per sample	**Abundance**** **relative fractions of each species abundance (ind./m^2) to mean biomass per sample
nMDS plots based on Bray-Curtis similarity	Stress: 0.218  	Stress: 0.136 
	Stress: 0.146  	Stress: 0.197 
	Stress: 0.208  	Stress: 0.172 

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Biomass*

*relative fractions of each species biomass (g/m^2) to mean biomass per sample

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Abundance**

**relative fractions of each species abundance (ind./m^2) to mean biomass per sample

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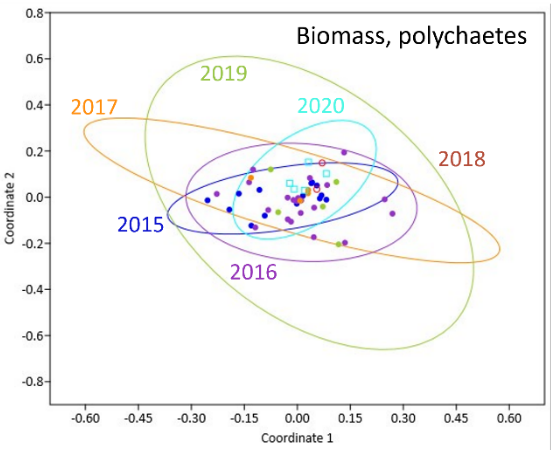
Stress: 0.237



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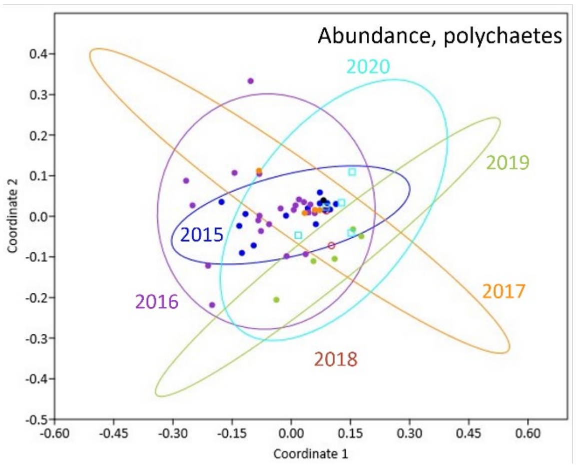
Stress: 0.125



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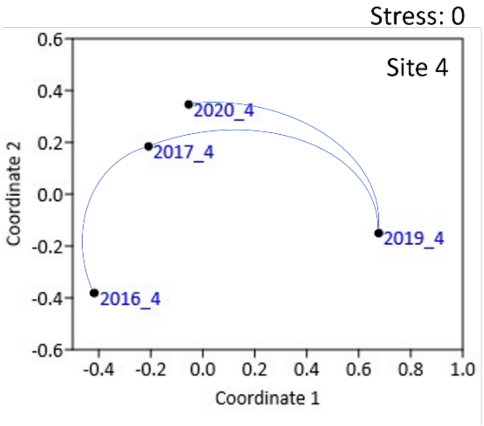
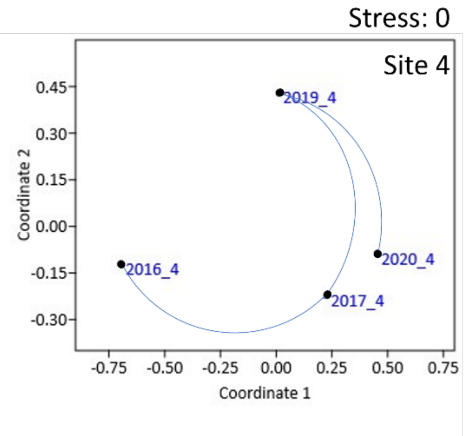
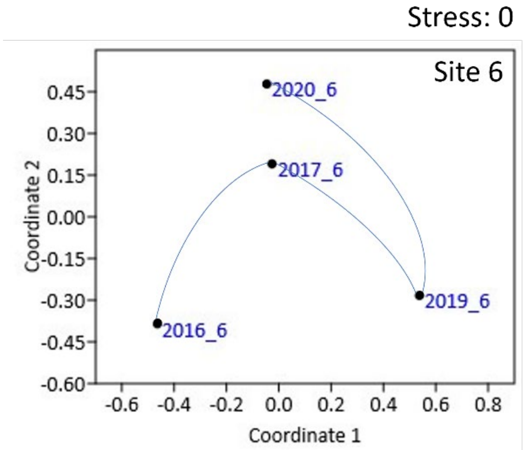
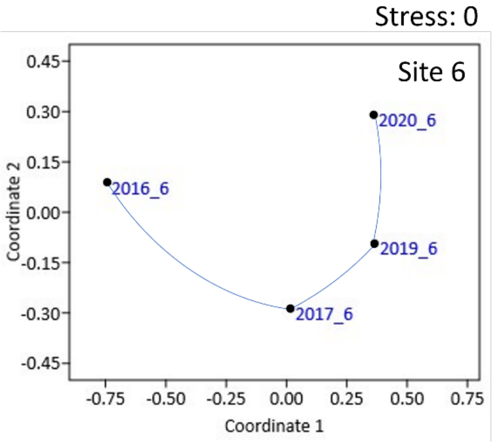
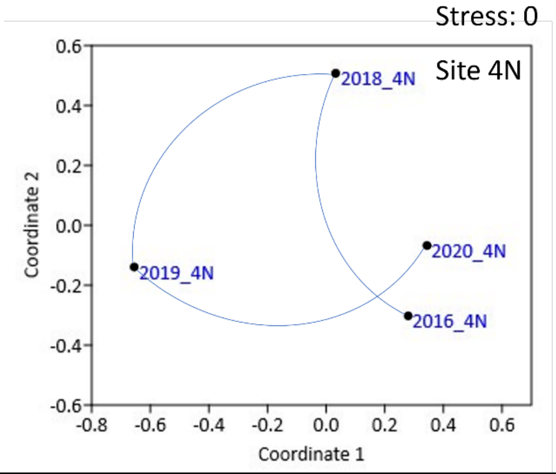
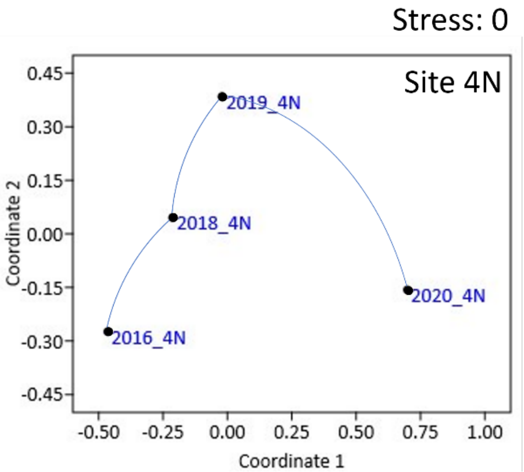
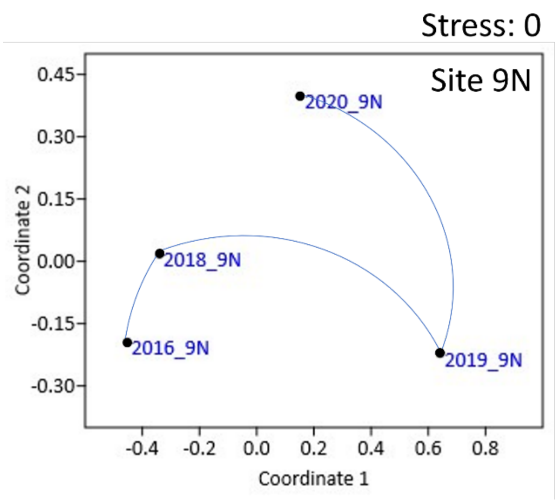
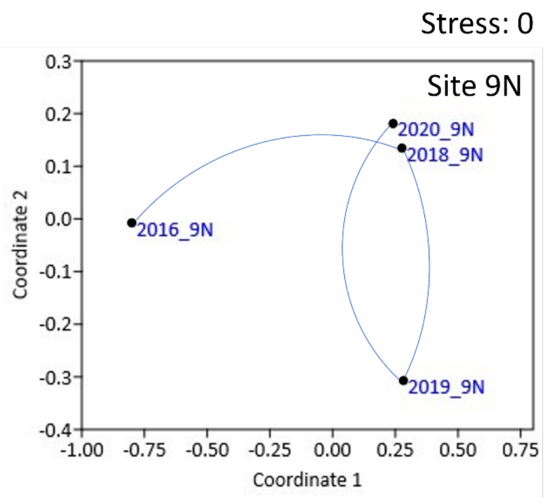
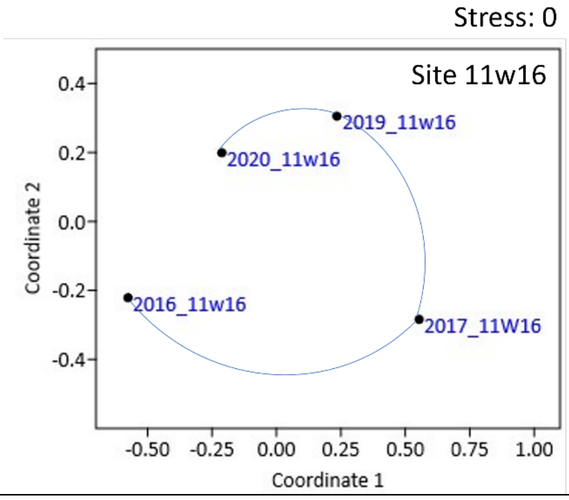
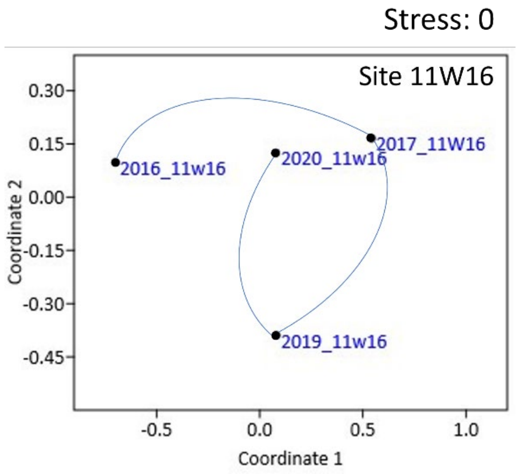
Appendix 2-4. nMDS plots for individual sites that were sampled for more than two years

	Biomass* *relative fractions of each species biomass (g/m²) to mean biomass per sample	**Abundance**** **relative fractions of each species abundance (ind./m²) to mean biomass per sample
nMDS plots based on Bray-Curtis similarity		
		
		

	Stress: 0 Site 9N 2020_9N 2018_9N 2016_9N 2019_9N Coordinate 2 Coordinate 1 0.45 0.30 0.15 0.00 -0.15 -0.30 -0.4 -0.2 0.0 0.2 0.4 0.6 0.8	Stress: 0 Site 9N 2020_9N 2018_9N 2016_9N 2019_9N Coordinate 2 Coordinate 1 0.3 0.2 0.1 0.0 -0.1 -0.2 -0.3 -0.4 -1.00 -0.75 -0.50 -0.25 0.00 0.25 0.50 0.75
	Stress: 0 Site 11w16 2019_11w16 2020_11w16 2016_11w16 2017_11W16 Coordinate 2 Coordinate 1 0.4 0.2 0.0 -0.2 -0.4 -0.50 -0.25 0.00 0.25 0.50 0.75 1.00	Stress: 0 Site 11W16 2017_11W16 2016_11w16 2020_11w16 2019_11w16 Coordinate 2 Coordinate 1 0.30 0.15 0.00 -0.15 -0.30 -0.45 -0.5 0.0 0.5 1.0

Appendix 2-5. Species presence/absence matrix per years

Class	Taxa (species / genus / family)	2015	2016	2017	2018	2019	2020
		presence/absence					
Anthozoa	*Limnactinia laevis*	0	1	0	0	0	0
Anthozoa	Octocorallia Gen.sp.	1	0	0	0	0	0
Anthozoa	Actiniidae Gen.sp.	0	1	0	0	0	1
Anthozoa	*Cerianthus lloydii*	1	0	1	0	1	1
Anthozoa	Edwardsiidae Gen. sp.	0	0	0	1	0	0
Anthozoa	*Gersemia* sp.	0	0	0	1	0	0
Aplacophora	*Chaetodermis* sp.	0	0	1	0	1	1
Aplacophora	*Chaetodermis penicilligerus*	0	0	0	1	0	0
Aplacophora	Solenogastres Gen.sp.	1	1	0	0	0	0
Ascidiacea	*Eugyra pedunculata*	1	0	0	0	0	0
Ascidiacea	*Pelonaia corrugata*	0	1	0	0	0	0
Bivalvia	*Astarte borealis*	1	1	1	1	1	1
Bivalvia	*Astarte crenata*	0	0	1	1	1	1
Bivalvia	*Astarte elliptica*	1	1	0	0	0	0
Bivalvia	*Astarte montagui*	1	1	1	0	0	0
Bivalvia	*Ciliatocardium ciliatum*	1	1	1	1	1	1
Bivalvia	*Crenella decussata*	0	1	0	0	0	0
Bivalvia	*Ennucula tenuis*	1	1	1	1	1	1
Bivalvia	*Hiatella arctica*	0	1	0	1	1	0
Bivalvia	*Limecola balthica*	0	0	0	1	0	0
Bivalvia	*Liocyma fluctuosa*	0	0	0	0	0	1
Bivalvia	*Lyonsia arenosa*	0	0	0	0	0	1
Bivalvia	*Macoma calcarea*	1	1	1	1	1	1
Bivalvia	*Macoma loveni*	0	0	0	0	0	1
Bivalvia	*Macoma* sp.	0	0	0	1	0	0
Bivalvia	*Modiolus modiolus*	0	1	1	1	0	0
Bivalvia	*Musculus glacialis*	1	1	0	0	1	1
Bivalvia	*Musculus niger*	1	0	0	1	0	0
Bivalvia	*Mya pseudoarenaria*	0	0	1	0	0	0
Bivalvia	*Mya truncata*	1	1	0	1	1	1
Bivalvia	Mytilidae Gen. sp.	0	0	0	1	0	0
Bivalvia	*Nuculana minuta*	1	1	1	0	0	0
Bivalvia	*Nuculana pernula*	0	1	1	0	1	1
Bivalvia	*Pandora glacialis*	1	1	1	0	0	0
Bivalvia	*Portlandia arctica*	0	0	1	0	0	0
Bivalvia	*Serripes groenlandicus*	1	1	1	1	1	1
Bivalvia	*Thyasira flexuosa*	1	0	0	0	0	0
Bivalvia	*Thyasira gouldi*	0	0	0	1	0	0
Bivalvia	*Thyasira sarsi*	1	1	1	0	1	1
Bivalvia	*Yoldia hyperborea*	1	1	1	1	1	1
Bivalvia	*Yoldiella lenticula*	0	1	1	0	1	0
Bivalvia	*Yoldiella nana*	0	1	0	0	1	0
Gastropoda	*Admete viridula*	1	1	1	1	1	1
Gastropoda	*Ariadnaria borealis*	0	0	0	0	0	0
Gastropoda	*Astyris rosacea*	0	0	1	0	0	0
Gastropoda	*Buccinum ciliatum*	0	0	0	0	0	1
Gastropoda	*Buccinum scalariforme*	1	1	0	0	0	0
Gastropoda	*Buccinum* sp.	0	0	0	1	0	1
Gastropoda	*Buccinum undatum*	0	0	0	0	1	0
Gastropoda	*Cryptonatica affinis*	1	1	0	0	0	1

Class	**Taxa (species / genus / family)**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
		presence/absence					
Gastropoda	*Cylichna alba*	1	1	0	1	0	1
Gastropoda	*Cylichnoides occultus*	0	1	0	0	1	0
Gastropoda	*Euspira pallida*	1	1	0	0	0	0
Gastropoda	*Lacuna crassior*	0	0	0	0	1	0
Gastropoda	*Lacuna vincta*	0	0	1	0	0	0
Gastropoda	*Margarites costalis*	1	0	0	0	0	0
Gastropoda	*Margarites groenlandicus*	1	1	1	1	1	0
Gastropoda	*Margarites helicinus*	1	1	1	0	0	0
Gastropoda	*Moelleria costulata*	0	0	0	0	1	0
Gastropoda	*Neoiphinoe kroyeri*	0	1	0	0	0	0
Gastropoda	*Neptunea borealis*	0	0	1	0	0	0
Gastropoda	*Neptunea despecta*	1	1	0	0	0	0
Gastropoda	*Nucella lapillus*	0	1	0	0	0	0
Gastropoda	*Obesotoma simplex*	0	0	0	0	0	1
Gastropoda	*Oenopota* sp.	1	1	0	0	0	1
Gastropoda	*Onchidoris muricata*	0	0	0	0	0	1
Gastropoda	*Plicifusus kroyeri*	1	0	0	0	0	0
Gastropoda	*Praephiline finmarchica*	0	0	0	1	0	0
Gastropoda	*Propebela harpularia*	1	1	0	0	0	0
Gastropoda	*Retifusus latericeus*	0	0	0	0	1	0
Gastropoda	*Retusa* sp.	0	0	0	0	1	0
Gastropoda	*Retusophiline lima*	0	0	0	0	0	1
Gastropoda	Rissoidae Gen. sp.	0	0	0	1	0	0
Gastropoda	*Scaphander punctostriatus*	1	0	0	0	0	0
Gastropoda	*Setia latior*	0	1	0	0	0	0
Gastropoda	*Solariella obscura*	1	1	1	0	1	1
Gastropoda	*Solariella varicosa*	1	0	1	0	1	0
Gastropoda	Trochoidea Gen. sp.	0	0	0	1	0	0
Globothalamea	*Alveolophragmium orbiculatum*	0	1	0	0	0	0
Gymnolaemata	*Alcyonidium disciforme*	0	0	1	0	1	0
Gymnolaemata	*Alcyonidium gelatinosum*	0	0	1	0	0	0
Gymnolaemata	*Amathia gracilis*	0	0	1	0	0	0
Gymnolaemata	Gymnolaemata Gen.sp.	0	1	0	0	0	1
Gymnolaemata	*Celleporella hyalina*	0	0	1	0	0	0
Gymnolaemata	*Electra pilosa*	0	1	0	0	0	0
Gymnolaemata	*Eucratea loricata*	0	0	1	0	1	0
Hexanauplia	Harpacticoida Gen.sp.	1	0	0	0	0	0
Holothuroidea	*Myriotrochus rinkii*	0	0	1	0	0	0
Holothuroidea	*Pentamera calcigera*	0	0	0	1	0	1
Holothuroidea	*Psolus phantapus*	0	1	0	0	0	1
Holothuroidea	*Thyonidium drummondii*	0	1	0	0	0	0
Hoplonemertea	*Amphiporus* sp.	0	0	1	0	0	0
Hydrozoa	*Halitholus yoldiaearcticae*	1	0	0	0	0	0
Hydrozoa	Hydroidolina Gen.sp.	0	0	0	0	0	0
Hydrozoa	Hydrozoa rest	0	0	1	0	0	1
Hydrozoa	*Obelia longissima*	0	0	0	0	1	0
Malacostraca	*Arctolembos arcticus*	0	1	1	0	0	0
Malacostraca	*Brachydiastylis resima*	1	1	1	1	1	1
Malacostraca	*Byblis gaimardii*	1	1	1	1	1	1
Malacostraca	*Campylaspis* sp.	1	1	0	0	0	0
Malacostraca	*Campylaspis costata*	0	0	0	0	1	0
Malacostraca	*Campylaspis umbensis*	0	0	0	1	0	1

Class	**Taxa (species / genus / family)**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
		presence/absence					
Malacostraca	*Crassicorophium crassicorne*	1	0	0	0	0	0
Malacostraca	*Diastylis glabra*	0	1	1	0	0	1
Malacostraca	*Diastylis rathkei*	1	1	1	0	0	0
Malacostraca	*Diastylis* sp.juv	0	0	0	1	0	1
Malacostraca	*Diastylis sulcata*	1	1	1	0	1	0
Malacostraca	Dulichiidae Gen.sp.	0	0	0	1	0	0
Malacostraca	*Dyopedos bispinis*	0	0	0	0	1	1
Malacostraca	*Dyopedos porrectus*	0	0	1	0	0	0
Malacostraca	*Eudorella emarginata*	1	0	0	0	0	1
Malacostraca	*Eurythenes gryllus*	0	1	0	0	0	0
Malacostraca	*Haploops tubicola*	1	1	1	0	0	0
Malacostraca	*Harpinia* sp.	0	0	0	1	0	0
Malacostraca	*Hyas araneus*	0	1	0	0	1	1
Malacostraca	*Ischyrocerus anguipes*	0	0	0	0	0	1
Malacostraca	*Lamprops fuscatus*	1	1	1	1	1	1
Malacostraca	*Leptostylis macrura*	0	1	0	0	0	0
Malacostraca	*Leucon nasica*	0	0	0	0	1	1
Malacostraca	*Leucon pallidus*	1	1	0	0	0	0
Malacostraca	*Leucon* sp.juv	0	0	0	1	0	0
Malacostraca	Lysianassidae Gen.sp.	0	1	0	1	0	0
Malacostraca	*Maera danae*	1	0	0	0	0	1
Malacostraca	*Maera loveni*	0	0	0	0	1	0
Malacostraca	*Megamoera dentata*	1	1	1	0	0	1
Malacostraca	*Melita palmata*	0	0	1	1	0	1
Malacostraca	*Melita* sp.	0	0	0	1	0	0
Malacostraca	*Metopa* sp.	1	1	1	0	1	1
Malacostraca	*Monoculodes* sp.	1	1	1	1	0	0
Malacostraca	*Munna fabricii*	0	0	0	0	0	0
Malacostraca	*Odius carinatus*	0	0	0	0	0	1
Malacostraca	Oedicerotidae Gen.sp.	0	0	0	1	0	1
Malacostraca	*Orchomenella* sp.	1	0	0	0	0	1
Malacostraca	*Pagurus pubescens*	0	1	0	1	1	1
Malacostraca	*Pandalus borealis*	0	0	0	1	0	0
Malacostraca	*Petalosarsia declivis*	0	0	1	0	0	0
Malacostraca	*Photis reinhardi*	0	0	0	0	0	1
Malacostraca	*Pleurogonium rubicundum*	0	0	0	0	1	0
Malacostraca	*Pleurogonium* sp.	1	0	0	0	0	1
Malacostraca	*Pontoporeia femorata*	1	1	1	1	0	0
Malacostraca	*Priscillina armata*	1	0	0	0	0	0
Malacostraca	*Protomedeia fasciata*	1	1	1	1	0	1
Malacostraca	*Protomedeia grandimana*	0	0	0	1	1	1
Malacostraca	*Rostroculodes schneideri*	0	0	0	0	0	1
Malacostraca	*Acanthonotozoma inflatum*	0	0	0	1	0	0
Malacostraca	*Aceroides latipes*	0	0	0	0	1	1
Malacostraca	*Akanthophoreus gracilis*	1	0	0	1	0	1
Malacostraca	*Ampelisca macrocephala*	1	1	1	1	0	0
Malacostraca	*Ampithoe rubricata*	0	0	1	0	0	0
Malacostraca	*Anonyx nugax*	1	0	0	0	1	0
Malacostraca	*Aoroides* sp.	0	1	0	0	0	0
Malacostraca	*Rozinante fragilis*	0	1	0	0	0	0
Malacostraca	Stenothoidae Gen.sp. Juv	0	0	0	1	0	0
Malacostraca	*Synidotea* sp	0	1	0	0	0	1

Class	Taxa (species / genus / family)	2015	2016	2017	2018	2019	2020
		presence/absence					
Malacostraca	Synopiidae Rest	0	0	0	1	0	0
Malacostraca	*Syrrhoe crenulata*	1	0	0	1	0	0
Nematoda	Nematoda Gen.sp.	1	1	1	0	0	0
Nemertea	Nemertea Gen.sp.	1	1	1	1	1	1
Nemertea	*Poseidon* sp.	0	0	1	0	0	0
Nodosariata	*Enantiodentalina obliqua*	0	0	1	0	0	0
Ophiuroidea	*Amphiura* sp.	0	0	1	0	0	0
Ophiuroidea	*Ophiacantha bidentata*	0	1	0	0	0	0
Ophiuroidea	*Ophiocten sericeum*	0	1	0	0	0	0
Ophiuroidea	*Ophiura sarsii*	0	0	1	0	0	0
Ophiuroidea	*Stegophiura nodosa*	1	1	0	0	0	0
Ostracoda	Ostracoda Gen.sp.	0	0	1	0	1	1
Pilidiophora	*Lineus* sp.	0	0	0	0	1	0
Pilidiophora	*Micrura* sp.	0	0	0	0	1	0
Platyhelminthes	Platyhelminthes Gen. sp.	0	0	0	1	0	0
Polychaeta	*Aglaophamus malmgreni*	1	0	0	1	0	0
Polychaeta	*Ampharete acutifrons*	0	0	1	0	0	0
Polychaeta	*Ampharete borealis*	0	1	1	0	1	0
Polychaeta	*Ampharete falcata*	0	0	0	0	1	1
Polychaeta	*Ampharete finmarchica*	0	1	0	0	0	0
Polychaeta	*Ampharete lindstroemi*	0	1	0	0	0	0
Polychaeta	*Ampharete* sp.	1	1	0	1	0	1
Polychaeta	Ampharetidae Gen.sp.	1	0	1	0	0	0
Polychaeta	*Amphicteis gunneri*	0	1	0	0	0	0
Polychaeta	*Amphicteis ninonae*	0	1	0	0	0	0
Polychaeta	*Amphicteis sundevalli*	0	0	0	0	0	0
Polychaeta	*Amphitrite* sp.	0	0	0	1	0	0
Polychaeta	*Amythasides macroglossus*	0	1	0	0	0	0
Polychaeta	*Anobothrus gracilis*	0	1	1	0	0	0
Polychaeta	*Aphelochaeta marioni*	1	1	1	0	0	0
Polychaeta	*Apistobranchus tullbergi*	0	1	1	1	1	1
Polychaeta	*Aricidea nolani*	1	1	1	1	1	1
Polychaeta	*Artacama proboscidea*	1	1	1	1	1	1
Polychaeta	*Axiothella catenata*	1	1	1	0	1	0
Polychaeta	*Brada granulosa*	0	0	0	1	0	0
Polychaeta	*Brada strelzovi*	1	0	0	0	0	0
Polychaeta	*Bradabyssa villosa*	1	1	1	1	1	1
Polychaeta	*Bylgides* sp.	1	0	1	0	0	1
Polychaeta	*Capitella capitata*	1	1	1	1	1	1
Polychaeta	Capitellidae Gen.sp.	1	0	0	0	0	0
Polychaeta	*Chaetozone setosa*	1	1	1	0	1	1
Polychaeta	*Chone* sp.	1	1	0	1	1	1
Polychaeta	Cirratulidae Gen.sp.	1	0	0	1	0	0
Polychaeta	*Cirratulus cirratus*	1	0	1	0	0	0
Polychaeta	*Cistenides hyperborea*	1	1	1	1	1	1
Polychaeta	*Clymenura polaris*	1	1	1	0	0	0
Polychaeta	*Cossura longocirrata*	1	1	1	1	1	1
Polychaeta	*Diplocirrus glaucus*	0	0	1	0	0	0
Polychaeta	*Diplocirrus longisetosus*	1	1	1	0	0	0
Polychaeta	*Dorvillea* sp.	0	0	0	0	0	1
Polychaeta	*Echiurus echiurus*	0	0	1	0	1	0
Polychaeta	*Enipo* sp.	0	0	1	0	0	0

Class	**Taxa (species / genus / family)**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
		presence/absence					
Polychaeta	*Enipo tamarae*	0	0	1	0	0	0
Polychaeta	*Eteone barbata*	1	1	1	0	1	0
Polychaeta	*Eteone flava*	1	1	1	1	1	1
Polychaeta	*Euchone analis*	0	0	1	1	0	0
Polychaeta	*Euchone papillosa*	0	1	0	0	0	0
Polychaeta	*Eulalia* sp.	0	1	0	0	0	0
Polychaeta	*Eunoe nodosa*	0	0	1	0	0	0
Polychaeta	*Eunoe* sp.	0	1	0	0	0	0
Polychaeta	*Flabelligera affinis*	0	1	0	0	1	0
Polychaeta	*Galathowenia oculata*	1	1	1	1	0	1
Polychaeta	*Gattyana cirrhosa*	0	0	1	0	0	0
Polychaeta	*Glycera capitata*	0	1	0	0	0	0
Polychaeta	*Hamingia arctica*	1	1	0	0	0	0
Polychaeta	*Harmothoe imbricata*	0	1	0	0	0	0
Polychaeta	*Harmothoe viridis*	0	0	0	0	1	0
Polychaeta	*Harmothoe* sp.	0	1	0	0	1	0
Polychaeta	*Hesperonoe laevis*	0	0	0	0	1	0
Polychaeta	*Heteroclymene robusta*	0	1	0	0	0	0
Polychaeta	*Heteromastus filiformis*	1	1	1	0	0	0
Polychaeta	*Heteromastus giganteus*	0	0	1	0	0	0
Polychaeta	*Lanassa nordenskioldi*	0	0	1	0	0	0
Polychaeta	*Laonice cirrata*	1	1	1	0	1	1
Polychaeta	*Laonice sarsi*	0	1	0	0	0	0
Polychaeta	*Laphania boecki*	0	1	0	0	0	0
Polychaeta	*Leaena ebranchiata*	0	0	1	0	0	1
Polychaeta	Lepidonotinae Gen.sp.	0	1	0	0	0	0
Polychaeta	*Leitoscoloplos acutus*	0	0	0	0	1	0
Polychaeta	*Levinsenia gracilis*	1	1	1	1	1	1
Polychaeta	*Lumbriclymene cylindricauda*	0	1	0	0	0	0
Polychaeta	*Lumbriclymene minor*	0	1	0	0	1	0
Polychaeta	*Lumbrineris latreilli*	0	1	0	0	0	0
Polychaeta	*Lumbrineris* sp.	0	1	0	0	0	0
Polychaeta	*Lysippe labiata*	1	1	1	1	1	1
Polychaeta	*Maldane sarsi*	1	1	1	0	1	1
Polychaeta	*Marenzelleria arctia*	0	0	1	0	0	0
Polychaeta	*Marenzelleria* sp.	1	0	0	0	0	0
Polychaeta	*Melinna elisabethae*	1	1	1	0	1	1
Polychaeta	*Micronephthys minuta*	1	1	1	1	1	1
Polychaeta	*Neoamphitrite groenlandica*	0	1	0	0	0	0
Polychaeta	*Neopolynoe paradoxa*	0	0	0	0	1	0
Polychaeta	Nephtyidae Gen. sp.	0	0	0	1	0	0
Polychaeta	*Nephtys caeca*	0	1	1	0	0	0
Polychaeta	*Nephtys ciliata*	1	1	1	1	1	1
Polychaeta	*Nephtys longosetosa*	0	0	1	0	0	0
Polychaeta	*Nephtys pente*	1	0	0	0	0	0
Polychaeta	*Nephtys* sp.	0	1	1	0	1	0
Polychaeta	*Nicomache lumbricalis*	0	1	1	0	0	0
Polychaeta	*Nicomache minor*	1	1	0	0	0	0
Polychaeta	*Notomastus latericeus*	0	0	1	0	0	1
Polychaeta	*Notomastus* sp.	1	0	0	0	1	0
Polychaeta	*Notoproctus oculatus*	0	1	0	0	0	0
Polychaeta	*Ophelia borealis*	1	0	0	0	0	0

Class	**Taxa (species / genus / family)**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
		presence/absence					
Polychaeta	*Ophelia limacina*	0	1	1	0	1	0
Polychaeta	*Ophelia* sp.	0	1	0	0	0	0
Polychaeta	*Ophelina acuminata*	1	1	0	1	1	1
Polychaeta	*Ophelina cylindricaudata*	0	0	0	1	0	0
Polychaeta	*Ophelina* sp.	0	0	0	1	0	0
Polychaeta	*Ophryotrocha* sp.	0	0	1	0	0	0
Polychaeta	*Owenia fusiformis*	1	1	0	0	0	0
Polychaeta	*Owenia polaris*	0	0	0	0	1	0
Polychaeta	*Paradoneis lyra*	1	0	1	0	0	0
Polychaeta	Paraonidae Gen. sp.	0	0	0	0	0	0
Polychaeta	*Paraonides nordica*	0	1	0	0	0	0
Polychaeta	*Pherusa* sp.	0	1	0	0	0	0
Polychaeta	*Pholoe longa*	0	1	0	1	1	1
Polychaeta	*Phyllodoce citrina*	0	1	0	0	0	0
Polychaeta	*Phyllodoce groenlandica*	1	1	1	1	1	1
Polychaeta	Phyllodocidae Gen.sp.	0	1	0	0	0	0
Polychaeta	*Polycirrus arcticus*	0	1	0	0	0	0
Polychaeta	*Polycirrus medusa*	0	1	0	0	0	0
Polychaeta	*Polydora* sp.	0	0	0	1	1	0
Polychaeta	Polynoidae Gen.sp.	1	0	1	1	0	1
Polychaeta	*Polyphysia crassa*	1	0	0	0	0	0
Polychaeta	*Praxillella affinis*	0	1	0	1	0	0
Polychaeta	*Praxillella gracilis*	1	1	1	0	1	1
Polychaeta	*Praxillella praetermissa*	1	1	1	1	1	1
Polychaeta	*Praxillura longissima*	0	1	0	0	0	0
Polychaeta	*Prionospio cirrifera*	0	1	0	0	0	0
Polychaeta	*Prionospio* sp.	0	1	0	0	1	1
Polychaeta	Pseudopolydora sp.	0	0	1	0	0	0
Polychaeta	*Pygospio elegans*	0	0	1	0	0	0
Polychaeta	*Rhodine* sp.	1	1	1	0	1	1
Polychaeta	Sabellidae Gen.sp.	1	0	0	0	0	0
Polychaeta	*Scalibregma inflatum*	1	1	1	1	1	1
Polychaeta	*Scalibregma robusta*	0	1	0	0	0	0
Polychaeta	*Scalibregma* sp.	0	1	0	0	0	0
Polychaeta	*Scolelepis foliosa*	0	1	0	0	0	0
Polychaeta	*Scoletoma fragilis*	1	1	1	1	1	1
Polychaeta	*Scoloplos armiger*	1	1	1	1	0	1
Polychaeta	Sphaerodoridae Gen.sp.	0	1	0	0	0	0
Polychaeta	*Spio armata*	0	1	0	0	0	0
Polychaeta	*Spio limicola*	1	1	1	1	1	1
Polychaeta	*Spio malmgreni*	0	1	0	0	0	0
Polychaeta	*Spio theeli*	0	0	1	0	0	0
Polychaeta	*Spiochaetopterus typicus*	1	1	1	0	1	1
Polychaeta	*Spiophanes* sp.	0	1	1	0	1	0
Polychaeta	Terebellidae Gen.sp.	1	1	1	0	0	1
Polychaeta	*Terebellides gracilis*	0	1	0	0	0	0
Polychaeta	*Terebellides stroemii*	1	1	1	1	1	1
Polychaeta	*Travisia forbesii*	1	0	1	1	0	0
Polychaeta	*Trichobranchus glacialis*	0	1	0	0	0	0
Polychaeta	*Trichobranchus* sp.	0	0	1	0	0	0
Priapulida	*Halicryptus spinulosus*	0	0	1	0	0	0
Priapulida	*Priapulus caudatus*	1	1	1	1	1	1

Class	**Taxa (species / genus / family)**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**
		presence/absence					
Pycnogonida	Pycnogonidae Gen.sp.	0	1	0	0	0	0
Pycnogonida	*Achelia borealis*	0	0	1	0	0	0
Pycnogonida	*Nymphon macronyx*	0	0	0	1	0	0
Pycnogonida	Nymphonidae Gen.sp.	1	0	0	0	1	1
Rhynchonellata	*Hemithiris psittacea*	0	1	0	0	0	0
Sipunculidea	*Golfingia margaritacea*	1	1	1	1	0	0
Sipunculidea	*Phascolion strombus*	0	1	0	0	0	0
Sipunculidea	Sipunculidea Gen.sp.	1	0	0	0	1	1
Stenolaemata	*Entalophora* sp.	0	0	0	0	1	0
Thecostraca	*Balanus balanus*	0	0	0	0	1	1
Tubothalamea	*Cornuspira* sp.	0	0	1	0	0	0

Appendix 2-6. Raw abundance and biomass data

Raw abundance and biomass data used in the analyses in Chapter 2 are available open access via the links below.

Abundance data: https://cloud.m-rc.ru/s/ReoEfpotYtjXX4K
Biomass data: https://cloud.m-rc.ru/s/ieHpR3fjDtnDc6P

Biomass data key:

- Columns in this table represent sampling sites (values from multiple grabs averaged per site per year).
- Rows represent invertebrate taxa identified to the lowest taxonomical rank possible (species, if not possible - genus, if not possible - family).
- Values are biomass of species per sampling site in g/m^2.

Abundance data key:

- Columns in this table represent sampling sites (values from multiple grabs averaged per site per year).
- Rows represent invertebrate taxa identified to the lowest taxonomical rank possible (species, if not possible - genus, if not possible - family).
- Values are abundance of species per sampling site in ind./m^2.

Chapter 3

Appendix 3-1. Main characteristics* of ROV video recordings and decapod occurrences data

*Starting and finishing coordinates of each transect; correspondence to the nearest benthic site; total recording time; meaningful time - excluding non-readable fragments of video recordings, where the seabed was not visible and when the camera was stationary; number of all decapods registered, and number of each species identified; occurrence of decapods ind./min.

2016

Video	**Benthic site**	**Starting coordinates (degrees, decimal minutes, N; E)**		**Finishing coordinates (degrees, decimal minutes, N: E)**		**Date of recording***	**Recording time, sec**	**Meaningful time, sec**
Vide	1	69°27.195'	58°33.672'	69°27.193'	58°33.660'	09.07.2016	616	551
Vide	6	69°26.737'	58°09.819'	69°26.734'	58°09.814'	09.07.2016	556	350
Vide	10	69°36.440'	58°06.223'	69°36.437'	58°06.224'	09.07.2016	557	475
Vide	1w11	69°35.115'	58°31.236'	69°35.114'	58°31.249'	09.07.2016	597	329
Vide	11	69°37.568'	58°55.385'	69°37.565'	58°55.396'	09.07.2016	484	87
Vide	ROV6	69°51.470'	59°11.691'	69°51.469'	59°11.690'	10.07.2016	278	178
Vide	1N	69°43.719'	59°25.806'	69°43.716'	59°25.803'	10.07.2016	579	276
Vide	3N	69°42.249'	58°46.377'	69°42.246'	58°46.360'	10.07.2016	670	568
Vide	4N	69°45.640'	58°57.334'	69°45.632'	58°57.331'	10.07.2016	525	410
Vide	6N	69°48.647'	58°54.712'	69°48.643'	58°54.706'	10.07.2016	587	464
Vide	10N	69°51.840'	58°54.339'	69°51.836'	58°54.312'	11.07.2016	607	534
Vide	9N	69°50.728'	58°45.817'	69°50.729'	58°45.816'	11.07.2016	561	476
Vide	8N	69°49.034'	58°27.680'	69°49.034'	58°27.674'	11.07.2016	556	478
Vide	12N	69°54.414'	58°30.867'	69°54.413'	58°30.863'	11.07.2016	591	489
Vide	11N1	69°55.629'	58°41.637'	69°55.627'	58°41.645'	11.07.2016	575	274
Vide	11N2	69°56.819'	58°44.136'	69°56.820'	58°44.139'	11.07.2016	518	108

*(day, month, year)

Video	**Total # of decapods**	**Snow crab *Chionoecetes opilio***	**Spider crab *Hyas* sp**	**Hermit crab *Pagurus* sp**	**Decapod unidentified**	**Decapod occurrence per minute**
Video 1	6	2	2	1	1	0.65
Video 2	6	1	0	4	1	1.03
Video 3	12	3	1	6	2	1.52
Video 4	10	4	1	3	2	1.82
Video 5	1	0	0	1	0	0.69
Video 6	4	1	3	0	0	1.35
Video 7	7	0	2	3	2	1.52
Video 8	14	0	0	14	0	1.48
Video 9	19	2	5	12	0	2.78
Video 10	26	5	3	17	1	3.36
Video 11	21	2	2	16	1	2.36
Video 12	33	2	9	21	1	4.16
Video 13	17	2	2	11	2	2.13
Video 14	34	3	2	28	1	4.17
Video 15	25	4	2	16	3	5.47
Video 16	21	3	0	17	1	11.67

2020

Video	**Benthic site**	**Starting coordinates (degrees, decimal minutes, N; E)**		**Finishing coordinates (degrees, decimal minutes, N; E)**		**Date* of recording**	**Recording time, sec**	**Meaningful time, sec**
Video 1	4N	69°45,603’	58°57,391’	69°45,196	58°57,049	08.07.2020	427	244
Video 2	4N	69°45,603’	58°57,391’	69°45,196	58°57,049	08.07.2020	195	116
Video 3	9N	69°50,739’	58°45,842’	69°51,031	58°45,975	08.07.2020	341	115
Video 4	9N	69°50,739’	58°45,842’	69°51,031	58°45,975	08.07.2020	340	104
Video 5	4	69°18,656’	57°11,268’	69°18,652	57°12,534	15.07.2020	357	60
Video 8	11w16	69°36,469’	58°29,402’	69°36,614	58°29,630	15.07.2020	530	319
Video 9	11w16	69°36,469’	58°29,402’	69°36,614	58°29,630	15.07.2020	388	159
Video 12	6	69°31,477’	58°07,969’	69°31,451	58°08,377	15.07.2020	470	239

*(day, month, year)

Video	**Total # of decapods**	**Snow crab *Chionoecetes opilio***	**Spider crab *Hyas sp***	**Hermit crab *Pagurus sp***	**Decapod unidentified**	**Decapod occurrence per minute**
Video 1	8	0	0	8	0	1.03
Video 2	2	0	0	2	0	10.43
Video 3	20	0	1	19	0	7.50
Video 4	13	2	2	9	0	6.00
Video 5	6	2	1	2	1	3.01
Video 8	16	6	0	10	0	3.02
Video 9	8	2	1	4	0	1.00
Video 12	4	3	9	1	0	4.25

Appendix 3-2. Biological characteristics* of decapod specimens

*CL – Carapace Length; CW – Carapace Width, CH – Carapace Height (Depth); ChL – Chela Length; ChH – Chela Height (Depth); W – Weight.

№	Site	Year	Specimen	Sex	CL, mm	CW, mm	CH, mm	ChL, mm	ChH, mm	W, g	Stomach fullness, %
1	4N	2017	*C.opilio-01*	f	32.0	31.0	11.0	14.0	2.0	11.5	25%
2	4N	2017	*C.opilio-02*	m	36.0	35.0	14.0	13.0	2.5	13	45%
3	4N	2017	*C.opilio-03*	m	34.0	38.0	15.0	23.0	4.0	-	30%
4	9N	2017	*C.opilio-04*	f	33.0	32.0	12.0	14.0	2.5	13	30%
5	9N	2017	*C.opilio-05*	f	32.0	32.0	11.0	14.0	2.0	12.5	75%
6	9N	2017	*C.opilio-06*	m	29.0	28.0	10.5	14.0	2.0	8.5	5%
7	9N	2017	*C.opilio-07*	m	36.0	35.0	13.0	18.0	3.0	13	2%
8	9N	2017	*C.opilio-08*	m	31.0	29.0	11.0	16.0	2.5	10	3%
9	9N	2017	*C.opilio-09*	f	28.5	27.5	11.0	10.0	1.5	8	15%
10	9N	2017	*C.opilio-10*	m	31.0	30.0	11.0	19.0	3.0	11	70%
11	9N	2017	*C.opilio-11*	f	39.5	39.0	14.0	-	-	16.5	25%
12	9N	2017	*C.opilio-12*	m	32.0	30.5	11.0	18.5	2.5	12.0	65%
13	9N	2017	*C.opilio-13*	f	32.0	29.0	11.0	14.0	2.0	8.5	9%
14	9N	2017	*C.opilio-14*	m	30.0	28.0	11.0	18.5	3.0	10.0	5%
15	9N	2017	*C.opilio-15*	f	42.0	42.0	16.0	22.0	3.5	20.9	65%
16	9N	2017	*C.opilio-16*	m	30.5	29.0	10.5	17.0	2.0	9.4	5%
17	9N	2017	*C.opilioo-17*	f	32.5	31.0	11.0	17.0	2.0	9.5	7%
18	9N	2017	*C.opilio-18*	f	26.0	24.5	9.5	12.5	1.8	6.0	5%
19	9N	2017	*C.opilio-19*	m	33.0	31.0	13.0	19.0	3.0	13.0	40%
20	9N	2017	*C.opilio-20*	m	32.0	31.0	11.0	18.0	3.0	10.5	5%
21	9N	2017	*C.opilio-21*	m	29.0	28.0	11.0	18.0	4.0	7.5	2%
22	9N	2017	*C.opilio-22*	f	28.0	24.0	9.5	-	-	5.5	25%
23	9N	2017	*C.opilio-23*	m	27.0	26.0	10.0	14.0	2.0	7.5	9%
24	4N	2017	*H. araneus-1*	m	47.0	33.0	19.0	20.0	5.0	25	9%
25	4N	2017	*H. araneus-2*	m	45.0	32.0	16.0	20.0	6.0	19.5	90%
26	4N	2017	*H. araneus-3*	m	47.0	30.0	15.0	21.0	5.0	18.5	4%
27	4N	2017	*H. araneus-4*	m	46.0	33.0	16.0	17.5	5.0	20	70%
28	4N	2017	*H. araneus-5*	f	48.0	35.0	16.0	-	-	20	95%
29	4N	2017	*H. araneus-6*	m	48.0	33.0	16.0	-	-	18.5	40%
30	9N	2017	*H. araneus-7*	f	58.0	43.0	21.5	27.5	7.0	38.5	90%
31	9N	2017	*H. araneus-8*	m	56.0	41.0	23.0	28.0	8.0	41.5	90%
32	9N	2017	*H. araneus-9*	m	28.0	18.0	18.0	12.0	3.0	4.0	5%
33	4N	2017	*P. pubescens-01*	m	11.5			16.0	6.0	11.5	85%
34	4N	2017	*P. pubescens-02*	f	12.5			20.0	11.0	13.0	80%
35	4N	2017	*P. pubescens-03*	f	9.0			9.0	5.0	5.0	75%
36	4N	2017	*P. pubescens-04*	m	11.0			17.0	9.0	10.0	80%
37	4N	2017	*P. pubescens-05*	m	11.0			17.5	8.5	9.5	85%
38	4N	2017	*P. pubescens-06*	m	11.0			18.0	8.5	9.5	85%
39	4N	2017	*P. pubescens-07*	m	9.0			14.5	7.0	7.5	80%

№	Site	Year	Specimen	Sex	CL, mm	CW, mm	CH, mm	ChL, mm	ChH, mm	W, g	Stomach fullness, %
40	4N	2017	*P. pubescens-08*	m	4.5			-	-	-	80%
41	4N	2017	*P. pubescens-09*	m	9.0			-	-	-	60%
42	4N	2017	*P. pubescens-10*	m	8.5			11.0	5.0	4.0	65%
43	4N	2017	*P. pubescens-11*	f	5.0			7.0	3.0	1.5	40%
44	4N	2017	*P. pubescens-12*	f	4.0			5.0	1.5	1.0	70%
45	4N	2017	*P. pubescens-13*	m	4.0			-	-	-	75%
46	9N	2017	*P. pubescens-14*	m	11.0			14.0	5.5	8.5	50%
47	9N	2017	*P. pubescens-15*	m	12.0			18.0	9.0	11.5	35%
48	9N	2017	*P. pubescens-16*	f	8.5			12.0	6.0	6.0	15%
49	9N	2017	*P. pubescens-17*	m	12.0			22.0	10.0	13.0	70%
50	9N	2017	*P. pubescens-18*	m	9.0			15.0	6.0	7.0	25%
51	9N	2017	*P. pubescens-19*	m	11.0			18.5	9.0	8.0	30%
52	9N	2017	*P. pubescens-20*	f	8.0			-	-	-	55%
53	9N	2017	*P. pubescens-21*	m	11.0			16.0	5.0	6.5	70%
54	9N	2017	*P. pubescens-22*	f	7.5			11.0	4.0	2.5	40%
55	9N	2017	*P. pubescens-23*	m	12.0			19.0	7.0	9.5	70%
56	9N	2017	*P. pubescens-24*	f	10.0			19.0	8.0	8.0	70%
57	9N	2017	*P. pubescens-25*	m	9.5			15.0	7.0	6.5	70%
58	9N	2017	*P. pubescens-26*	m	10.0			18.0	8.0	8.0	65%
59	9N	2017	*P. pubescens-27*	m	12.5			29.0	12.5	16.5	55%
60	9N	2017	*P. pubescens-28*	m	8.0			10.0	5.5	3.0	60%
61	9N	2017	*P. pubescens-29*	m	8.0			11.0	4.0	3.5	76%
62	9N	2017	*P. pubescens-30*	m	8.0			11.0	5.0	3.0	80%
63	9N	2017	*P. pubescens-31*	f	8.5			10.0	5.0	3.0	55%
64	9N	2017	*P. pubescens-32*	f	8.0			11.0	4.0	3.0	50%
65	9N	2017	*P. pubescens-33*	m	7.0			6.5	2.0	2.0	45%
66	9N	2017	*P. pubescens-34*	f	9.0			11.0	5.0	3.0	40%
67	9N	2017	*P. pubescens-35*	m	9.0			14.5	7.0	5.5	60%
68	9N	2017	*P. pubescens-36*	m	5.0			-	-	-	65%
69	9N	2017	*P. pubescens-37*	m	11.0			7.5	4.0	1.5	35%
70	9N	2017	*P. pubescens-38*	m	6.0			9.0	4.5	2.0	50%
71	9N	2017	*P. pubescens-39*	m	6.5			8.5	4.0	2.0	45%
72	9N	2017	*P. pubescens-40*	m	5.0			-	-	-	40%
73	9N	2017	*P. pubescens-41*	m	4.0			-	-	-	35%
74	9N	2017	*P. pubescens-42*	m	4.5			-	-	-	50%
75	9N	2017	*P. pubescens-43*	m	4.5			-	-	-	10%

Appendix 3-3. Presence-absence of prey items and inclusions identified in stomach contents of *C. opilio*, *P. pubescens* and *H. araneus*

Diet composition	Taxa/species		Presence (p)/absence (a) in stomach contents of:		
			C. opilio	*P. pubescens*	*H. araneus*
(1) Prey items	**Bivalvia**		p	p	p
		Astarte eliptica	p	p	a
		Mytilus edulis agg	p	p	a
		Ciliatocardium	p	p	a
		Dacrydium vitreum	p	a	a
		Ennucula tenuis	p	p	a
		Macoma calcarea	p	a	a
	Annelida		p	p	p
		Pectinaria sp	a	a	p
		Maldanidae	p	a	a
		Owenia sp	p	a	a
		Cirratulidae	p	a	a
		Aphroditifornia	p	p	a
		Nephtys sp	a	a	p
	Gastropoda		p	p	a
		Margarites costalis	p	a	a
	Hydrozoa		p	p	p
		Obelia longissima	p	p	p
	Holothurioidea		p	p	p
		Cucumaria	a	p	a
	Foraminifera		p	p	a
		Cibicides refulgens	p	a	a
		Elphidium sp	a	p	a
		Elohidium	a	p	a
		Buccella frigida	a	p	a
		Pyrgo sp	a	p	a
	Crustacea		p	p	p
		Amphipoda	a	a	a
		Cirripedia	a	a	a
	Bryozoa		p	p	a
	Protista		p	p	a
	Aplacophora		a	p	p
	Nematoda		a	p	a
	Ostracoda		a	p	a
(2) Non-taxonomic categories	**Organic debris**		p	p	p
	Plant debris		p	p	a
	Eggs		p	p	a
(3) Inclusions	**Fat globules**		p	p	p
	Feathers		p	p	a
	Sand		p	p	p
	Plastics		p	p	p

Appendix 3-4. Raw data on stomach contents

Raw data om stomach contents used in diet analyses in Chapter 3 are available open access via the link below.

Stomach content data: https://cloud.m-rc.ru/s/DQ5HBg6adtpApFZ

Stomach content data key:

- Columns in this matrix represent prey categories (See Appendix 3-3).
- Rows represent decapod specimens.
- Values are percentage volume of each prey item in the food lump (visually estimated).

Chapter 4

Appendix 4-1. Catalogue of specimens studied for ingested microplastics

*Abbreviations: MP – microplastics; DGS – digestive system, MC – mantle cavity; G – gills; species ID: A.b. – *Astarte borealis*; A.e – *Astarte eliptica*; A.m – *Astarte montagui*; C.c – *Ciliatocardium ciliatum*; C.o – *Chionoecetes opilio*; H.a – *Hyas araneus*; N.p – *Nuculana pernula*; M.c – *Macoma calcarea*; M.e – *Mytilus edulis*; M.g – *Margarites groenlandicus*; P.a – *Portlandia arctica*; S.b – *Semibalanus balanoides*; S.g – *Serripes groenlandicus*; Y.h – *Yoldia hyperborea.*

Year	Sampling site	Specimen ID	Research area	L, mm	W, mm	H, mm	Weight, g	MP, n		
								DGS	MC	G
2008	1	A.b_17	Pechora Sea	40.00	32.00	12.00	11.05	1	0	0
2008	1	A.b_18	Pechora Sea	37.00	31.00	14.00	10.82	0	0	0
2008	1	C.c_24	Pechora Sea	45.00	40.00	25.50	17.50	0	0	0
2008	1	M.c_50	Pechora Sea	20.50	15.00	7.50	0.90	0	0	0
2008	3	C.c_04	Pechora Sea	40.00	41.50	26.00	16.34	0	3	0
2008	7	M.c_06	Pechora Sea	n/a	n/a	n/a	n/a	0	1	0
2008	7	M.c_07	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	7	M.c_08	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	7	M.c_09	Pechora Sea	n/a	n/a	n/a	n/a			
2008	7	Y.h_01	Pechora Sea	n/a	n/a	n/a	n/a	2	0	0
2008	9	M.c_26	Pechora Sea	14.00	10.00	4.50	0.19	0	0	0
2008	9	N.m_01	Pechora Sea	15.50	14.50	5.50	0.80	0	0	0
2008	9	N.m_02	Pechora Sea	28.00	24.50	10.50	4.12	2	2	0
2008	21	M.c_31	Pechora Sea	26.00	19.00	10.00	2.10	0	0	0
2008	21	M.c_32	Pechora Sea	24.00	16.50	9.50	1.53	0	0	0
2008	21	M.c_33	Pechora Sea	23.50	16.50	7.50	1.35	0	0	0
2008	21	M.c_34	Pechora Sea	19.00	14.00	5.50	0.66	0	0	0
2008	1(1)	C.c_16	Pechora Sea	26.00	24.00	16.00	5.52	0	0	0
2008	1(1)	C.c_17	Pechora Sea	41.00	39.00	24.00	15.42	0	0	0
2008	11(1)	A.b_13	Pechora Sea	40.00	34.00	13.50	13.26	0	0	0
2008	11(1)	A.b_14	Pechora Sea	35.00	30.00	14.00	10.06	0	0	0
2008	12(2)	A.b_12	Pechora Sea	40.00	35.00	15.00	14.00	0	2	0
2008	12(2)	C.c_10	Pechora Sea	24.00	23.00	14.00	2.73	0	0	0
2008	12(2)	C.c_11	Pechora Sea	21.50	20.00	15.00	4.57	0	0	0
2008	12(2)	C.c_12	Pechora Sea	38.00	39.00	24.00	14.60	0	0	0
2008	12(2)	C.c_13	Pechora Sea	40.00	41.00	23.00	17.34	0	0	0
2008	13(2)	C.c_15	Pechora Sea	43.00	40.00	22.00	14.21	0	0	0
2008	15(2)	C.c_25	Pechora Sea	26.00	24.00	15.50	3.42	0	0	0
2008	17(3)	M.c_14	Pechora Sea	25.00	18.00	8.00	n/a	0	0	0
2008	17(3)	M.c_15	Pechora Sea	24.50	18.00	8.50	n/a	0	0	0
2008	17(3)	M.c_16	Pechora Sea	16.00	13.00	6.00	n/a	0	1	0
2008	17(3)	M.c_17	Pechora Sea	17.50	14.50	5.50	n/a	0	0	0
2008	17(3)	M.c_18	Pechora Sea	20.00	15.00	5.50	n/a	0	0	0
2008	19(1)	A.b_07	Pechora Sea	44.00	32.00	13.50	19.20	0	0	0
2008	19(1)	C.c_08	Pechora Sea	25.00	24.00	15.00	4.57	0	0	0
2008	19(1)	A.b_11	Pechora Sea	42.00	35.00	16.50	16.74	0	0	0
2008	2(1)	C.c_06	Pechora Sea	46.00	45.00	25.50	17.56	0	1	0
2008	2(1)	C.c_09	Pechora Sea	43.00	42.00	27.00	14.34	0	0	0
2008	2(2)	C.c_07	Pechora Sea	44.00	38.00	24.00	17.37	0	4	0

Year	Sampling site	Specimen ID	Research area	L, mm	W, mm	H, mm	Weight, g	MP, n		
								DGS	MC	G
2008	2(3)	A.b_19	Pechora Sea	-	-	-	-	-	-	-
2008	2(3)	A.b_20	Pechora Sea	36.00	30.00	14.00	9.51	0	1	0
2008	23(1)	M.c_02	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	23(1)	M.c_03	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	23(1)	M.c_04	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	23(1)	M.c_05	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	23(1)	M.c_01	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	3(1)	C.c_05	Pechora Sea	40.00	39.80	24.80	16.90	0	0	0
2008	3(1)	A.b_36	Pechora Sea	34.00	27.50	12.00	6.63	0	0	0
2008	4(2)	A.b_05	Pechora Sea	35.50	29.00	13.20	8.29	0	1	0
2008	4(2)	M.c_19	Pechora Sea	22.50	15.00	7.50	0.99	0	0	0
2008	4(2)	M.c_20	Pechora Sea	22.00	15.00	7.50	1.04	0	0	0
2008	4(2)	M.c_21	Pechora Sea	24.50	19.00	8.00	1.59	0	0	0
2008	4(2)	M.c_22	Pechora Sea	21.00	15.50	8.50	1.17	2	0	0
2008	4(2)	M.c_23	Pechora Sea	20.00	13.00	5.50	0.61	0	0	0
2008	4(2)	M.c_24	Pechora Sea	19.00	13.50	6.50	0.67	0	0	0
2008	4(2)	M.c_25	Pechora Sea	21.00	15.00	6.50	1.01	0	0	0
2008	4(2)	A.b_10	Pechora Sea	40.00	35.00	11.50	17.44	0	0	0
2008	7(1)	M.c_10	Pechora Sea	n/a	n/a	n/a	n/a	1	0	0
2008	7(1)	M.c_11	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	7(1)	M.c_12	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	7(1)	M.c_13	Pechora Sea	n/a	n/a	n/a	n/a	0	0	0
2008	7(1)	M.c_44	Pechora Sea	18.00	15.00	8.50	0.55	0	0	1
2008	7(1)	M.c_45	Pechora Sea	20.00	18.00	6.00	0.59	0	0	0
2008	7(1)	M.c_46	Pechora Sea	20.00	20.00	8.50	0.81	0	0	0
2008	7(1)	M.c_47	Pechora Sea	21.00	17.50	6.00	0.42	0	0	0
2008	7(1)	M.c_48	Pechora Sea	20.00	15.00	7.50	0.75	0	0	0
2008	7(1)	M.c_49	Pechora Sea	20.50	10.00	5.00	0.23	0	0	0
2008	7(1)	N.m_15	Pechora Sea	24.00	20.00	11.00	0.17	0	0	0
2008	8(1)	A.b_24	Pechora Sea	43.00	37.00	16.00	17.61	0	1	0
2008	8(1)	S.b_1	Pechora Sea	17.00	20.00		2.89	0	0	0
2008	9(1)	A.b_08	Pechora Sea	40.00	34.00	17.50	17.31	0	0	0
2008	9(1)	A.b_09	Pechora Sea	35.00	38.00	14.50	7.91	1	1	0
2008	9(1)	N.m_06	Pechora Sea	25.00	21.00	10.00	3.18	0	0	0
2008	9(1)	M.c_27	Pechora Sea	19.50	15.00	6.50	0.72	0	0	0
2008	9(1)	M.c_28	Pechora Sea	20.50	15.00	7.50	1.05	0	0	0
2008	9(1)	M.c_29	Pechora Sea	11.50	12.50	6.00	0.45	1	0	0
2017	V1	C.o_04	Pechora Sea	33.0	32.0	2.5	13	1	n/a	0
2017	V1	C.o_05	Pechora Sea	32.0	32.0	2.0	12.5	0	n/a	0
2017	V1	C.o_06	Pechora Sea	29.0	28.0	2.0	8.5	0	n/a	0
2017	V1	C.o_07	Pechora Sea	36.0	35.0	3.0	13	0	n/a	0
2017	V1	C.o_08	Pechora Sea	31.0	29.0	2.5	10	0	n/a	0
2017	V1	C.o_09	Pechora Sea	28.5	27.5	1.5	8	0	n/a	0
2017	V1	C.o_10	Pechora Sea	31.0	30.0	3.0	11	1	n/a	0
2017	V1	C.o_11	Pechora Sea	39.5	39.0	-	16.5	1	n/a	0
2017	V1	C.o_12	Pechora Sea	32.0	30.5	2.5	12.0	0	n/a	0
2017	V1	C.o_13	Pechora Sea	32.0	29.0	2.0	8.5	0	n/a	0
2017	V1	C.o_14	Pechora Sea	30.0	28.0	3.0	10.0	0	n/a	0
2017	V1	C.o_15	Pechora Sea	42.0	42.0	3.5	20.9	1	n/a	0
2017	V1	C.o_16	Pechora Sea	30.5	29.0	2.0	9.4	0	n/a	0
2017	V1	C.o_17	Pechora Sea	32.5	31.0	2.0	9.5	1	n/a	0
2017	V1	C.o_18	Pechora Sea	26.0	24.5	1.8	6.0	0	n/a	0

Year	Sampling site	Specimen ID	Research area	L, mm	W, mm	H, mm	Weight, g	MP, n		
								DGS	MC	G
2017	V1	C.o_19	Pechora Sea	33.0	31.0	3.0	13.0	1	n/a	0
2017	V1	C.o_20	Pechora Sea	32.0	31.0	3.0	10.5	1	n/a	0
2017	V1	C.o_21	Pechora Sea	29.0	28.0	4.0	7.5	0	n/a	0
2017	V1	C.o_22	Pechora Sea	28.0	24.0	-	5.5	0	n/a	0
2017	V1	C.o_23	Pechora Sea	27.0	26.0	2.0	7.5	0	n/a	0
2017	V1	H.a_07	Pechora Sea	58.0	43.0	7.0	38.5	0	n/a	0
2017	V1	H.a_08	Pechora Sea	56.0	41.0	8.0	41.5	0	n/a	0
2017	V1	H.a_09	Pechora Sea	28.0	18.0	3.0	4.0	0	n/a	0
2017	V1	P.p_14	Pechora Sea	11.0		5.5	8.5	1	n/a	0
2017	V1	P.p_15	Pechora Sea	12.0		9.0	11.5	1	n/a	0
2017	V1	P.p_16	Pechora Sea	8.5		6.0	6.0	0	n/a	0
2017	V1	P.p_17	Pechora Sea	12.0		10.0	13.0	0	n/a	0
2017	V1	P.p_18	Pechora Sea	9.0		6.0	7.0	0	n/a	0
2017	V1	P.p_19	Pechora Sea	11.0		9.0	8.0	0	n/a	0
2017	V1	P.p_20	Pechora Sea	8.0		-	-	0	n/a	0
2017	V1	P.p_21	Pechora Sea	11.0		5.0	6.5	0	n/a	0
2017	V1	P.p_22	Pechora Sea	7.5		4.0	2.5	0	n/a	0
2017	V1	P.p_23	Pechora Sea	12.0		7.0	9.5	1	n/a	0
2017	V1	P.p_24	Pechora Sea	10.0		8.0	8.0	0	n/a	0
2017	V1	P.p_25	Pechora Sea	9.5		7.0	6.5	0	n/a	0
2017	V1	P.p_26	Pechora Sea	10.0		8.0	8.0	0	n/a	0
2017	V1	P.p_27	Pechora Sea	12.5		12.5	16.5	0	n/a	0
2017	V1	P.p_28	Pechora Sea	8.0		5.5	3.0	0	n/a	0
2017	V1	P.p_29	Pechora Sea	8.0		4.0	3.5	1	n/a	0
2017	V1	P.p_30	Pechora Sea	8.0		5.0	3.0	1	n/a	0
2017	V1	P.p_31	Pechora Sea	8.5		5.0	3.0	0	n/a	0
2017	V1	P.p_32	Pechora Sea	8.0		4.0	3.0	0	n/a	0
2017	V1	P.p_33	Pechora Sea	7.0		2.0	2.0	1	n/a	0
2017	V1	P.p_34	Pechora Sea	9.0		5.0	3.0	0	n/a	0
2017	V1	P.p_35	Pechora Sea	9.0		7.0	5.5	1	n/a	0
2017	V1	P.p_36	Pechora Sea	5.0		-	-	0	n/a	0
2017	V1	P.p_37	Pechora Sea	11.0		4.0	1.5	0	n/a	0
2017	V1	P.p_38	Pechora Sea	6.0		4.5	2.0	0	n/a	0
2017	V1	P.p_39	Pechora Sea	6.5		4.0	2.0	0	n/a	0
2017	V1	P.p_40	Pechora Sea	5.0		-	-	0	n/a	0
2017	V1	P.p_41	Pechora Sea	4.0		-	-	0	n/a	0
2017	V1	P.p_42	Pechora Sea	4.5		-	-	0	n/a	0
2017	V1	P.p_43	Pechora Sea	4.5		-	-	1	n/a	0
2017	V2	C.o_01	Pechora Sea	32.0	31.0	2.0	11.5	0	n/a	0
2017	V2	C.o_02	Pechora Sea	36.0	35.0	2.5	13	0	n/a	0
2017	V2	C.o_03	Pechora Sea	34.0	38.0	4.0	-	1	n/a	0
2017	V2	H.a_01	Pechora Sea	47.0	33.0	5.0	25	0	n/a	0
2017	V2	H.a_02	Pechora Sea	45.0	32.0	6.0	19.5	0	n/a	0
2017	V2	H.a_03	Pechora Sea	47.0	30.0	5.0	18.5	1	n/a	0
2017	V2	H.a_04	Pechora Sea	46.0	33.0	5.0	20	0	n/a	0
2017	V2	H.a_05	Pechora Sea	48.0	35.0	-	20	1	n/a	0
2017	V2	H.a_06	Pechora Sea	48.0	33.0	-	18.5	0	n/a	0
2017	V2	P.p_01	Pechora Sea	11.5		6.0	11.5	1	n/a	0
2017	V2	P.p_02	Pechora Sea	12.5		11.0	13.0	0	n/a	0
2017	V2	P.p_03	Pechora Sea	9.0		5.0	5.0	1	n/a	0
2017	V2	P.p_04	Pechora Sea	11.0		9.0	10.0	0	n/a	0
2017	V2	P.p_05	Pechora Sea	11.0		8.5	9.5	0	n/a	0

Year	Sampling site	Specimen ID	Research area	L, mm	W, mm	H, mm	Weight, g	MP, n		
								DGS	MC	G
2017	V2	P.p_06	Pechora Sea	11.0		8.5	9.5	0	n/a	0
2017	V2	P.p_07	Pechora Sea	9.0		7.0	7.5	1	n/a	0
2017	V2	P.p_08	Pechora Sea	4.5		-	-	1	n/a	0
2017	V2	P.p_09	Pechora Sea	9.0		-	-	0	n/a	0
2017	V2	P.p_10	Pechora Sea	8.5		5.0	4.0	0	n/a	0
2017	V2	P.p_11	Pechora Sea	5.0		3.0	1.5	1	n/a	0
2017	V2	P.p_12	Pechora Sea	4.0		1.5	1.0	0	n/a	0
2017	V2	P.p_13	Pechora Sea	4.0		-	-	0	n/a	0
2018	D1	S.g_01	Pechora Sea	27.50	23.00	15.30	3.01	0	0	0
2018	D1	S.g_02	Pechora Sea	23.00	20.00	12.50	2.02	1	0	0
2018	D1	S.g_03	Pechora Sea	22.80	20.00	12.00	1.86	1	0	0
2018	D1	S.g_04	Pechora Sea	19.80	16.00	10.20	1.09	0	0	0
2018	D1	S.g_05	Pechora Sea	9.50	8.00	5.80	0.15	0	0	0
2018	D1	C.c_01	Pechora Sea	20.00	19.00	11.00	1.92	0	0	0
2018	D1	Y.h_02	Pechora Sea	22.00	11.50	5.50	0.60	0	3	0
2018	D1	Y.h_03	Pechora Sea	24.00	14.00	6.00	0.77	0	0	0
2018	D1	Y.h_04	Pechora Sea	24.00	14.00	6.00	0.84	0	1	0
2018	D1	Y.h_05	Pechora Sea	26.00	15.50	6.20	1.01	0	0	0
2018	D1	Y.h_06	Pechora Sea	25.50	13.00	5.50	0.86	0	0	0
2018	D1	Y.h_07	Pechora Sea	23.00	11.50	5.50	0.65	0	1	0
2018	D1	A.b_03	Pechora Sea	40.00	34.50	13.50	13.85	0	3	0
2018	D1	Y.h_09	Pechora Sea	21.00	12.00	5.50	0.54	1	0	0
2018	D1	Y.h_10	Pechora Sea	21.50	12.00	5.50	0.58	0	1	0
2018	D1	Y.h_11	Pechora Sea	23.00	11.50	5.50	0.64	0	0	0
2018	D1	Y.h_12	Pechora Sea	25.00	13.00	6.00	0.77	0	0	0
2018	D1	Y.h_13	Pechora Sea	23.00	12.00	5.50	0.62	0	0	0
2018	D1	Y.h_14	Pechora Sea	25.00	13.00	6.00	0.96	0	0	0
2018	D1	S.g_7	Pechora Sea	22.00	18.00	12.00	2.05	1	0	0
2018	D1	M.c_30	Pechora Sea	41.00	30.00	15.00	12.52	0	0	0
2018	D1	N.m_07	Pechora Sea	12.00	10.00	7.50	1.12	0	0	0
2018	D1	Y.h_15	Pechora Sea	24.00	12.00	6.00	0.67	0	0	0
2018	D1	Y.h_16	Pechora Sea	24.00	12.00	5.50	0.58	0	0	0
2018	D1	Y.h_17	Pechora Sea	24.00	12.00	5.20	0.55	0	1	0
2018	D1	Y.h_18	Pechora Sea	22.00	11.00	5.00	0.55	0	0	0
2018	D1	Y.h_19	Pechora Sea	26.00	14.00	6.00	0.85	1	0	0
2018	D1	Y.h_20	Pechora Sea	23.00	13.00	6.00	0.68	0	0	0
2018	D1	Y.h_21	Pechora Sea	22.00	10.00	5.00	0.47	0	0	0
2018	D1	Y.h_22	Pechora Sea	23.00	11.00	5.00	0.55	1	0	0
2018	D1	Y.h_23	Pechora Sea	24.00	11.00	6.00	0.61	0	0	0
2018	D1	Y.h_24	Pechora Sea	24.00	12.00	6.00	0.58	0	0	0
2018	D1	Y.h_25	Pechora Sea	24.00	11.00	5.50	0.57	0	0	0
2018	D1	C.c_14	Pechora Sea	36.00	36.00	23.00	13.07	0	0	0
2018	D1	Y.h_26	Pechora Sea	21.00	11.00	5.50	0.46	0	0	0
2018	D1	Y.h_27	Pechora Sea	21.00	11.50	5.00	0.51	0	0	0
2018	D1	Y.h_28	Pechora Sea	21.00	10.50	5.00	0.42	0	0	0
2018	D1	Y.h_29	Pechora Sea	20.00	10.00	5.00	0.33	0	0	1
2018	D1	M.c_35	Pechora Sea	23.00	20.00	7.50	0.69	0	0	0
2018	D1	M.c_36	Pechora Sea	19.00	13.00	6.00	0.51	1	0	0
2018	D1	M.c_37	Pechora Sea	20.00	14.00	5.00	0.62	0	0	1
2018	D1	M.c_38	Pechora Sea	25.00	19.00	9.50	2.01	0	0	0
2018	D1	M.c_39	Pechora Sea	30.00	22.00	10.00	3.28	0	0	0
2018	D1	M.c_40	Pechora Sea	20.00	15.00	7.50	0.87	0	0	0

Year	Sampling site	Specimen ID	Research area	L, mm	W, mm	H, mm	Weight, g	MP, n		
								DGS	MC	G
2018	D1	Y.h_31	Pechora Sea	20.00	10.00	5.00	0.43	1	0	0
2018	D1	N.p_03	Pechora Sea	20.00	10.00	5.50	0.43	0	0	0
2018	D1	A.b_23	Pechora Sea	14.50	12.00	7.00	0.71	0	0	0
2018	D1	A.m_18	Pechora Sea	10.50	10.00	5.00	0.34	1	0	0
2018	D1	A.b_30	Pechora Sea	24.00	20.00	9.00	2.30	1	0	1
2018	D1	A.b_31	Pechora Sea	20.00	11.00	5.50	1.32	1	0	0
2018	D1	A.b_32	Pechora Sea	15.00	13.00	7.00	0.75	0	0	0
2018	D1	A.b_33	Pechora Sea	16.50	15.00	8.00	1.01	0	0	0
2018	D1	A.b_34	Pechora Sea	15.00	13.50	8.00	0.84	0	0	0
2018	D1	Y.h_32	Pechora Sea	23.00	10.20	4.00	0.66	1	0	0
2018	D1	Y.h_33	Pechora Sea	22.50	14.00	6.50	1.42	0	0	0
2018	D1	Y.h_34	Pechora Sea	22.50	11.00	5.00	0.68	1	1	0
2018	D1	Y.h_35	Pechora Sea	22.00	10.20	5.00	0.55	0	0	0
2018	D1	Y.h_36	Pechora Sea	23.00	10.00	5.00	0.56	1	0	0
2018	D2	S.g_06	Pechora Sea	70.00	64.50	37.50	51.40	0	0	0
2018	D2	A.b_35	Pechora Sea	32.00	27.00	11.50	7.11	1	0	0
2018	D2	M.g_2	Pechora Sea	24.50	21.50		4.42	0	0	0
2018	D2	A.m_19	Pechora Sea	11.50	10.00	5.00	0.33	2	0	0
2018	D2	A.m_20	Pechora Sea	12.00	10.00	5.50	0.37	1	0	0
2018	D2	A.m_21	Pechora Sea	11.00	10.00	5.00	0.29	0	0	0
2018	D2	A.m_22	Pechora Sea	10.00	8.50	5.00	0.23	2	0	0
2018	D2	A.m_23	Pechora Sea	11.50	10.00	5.50	0.40	1	0	0
2018	D2	A.m_24	Pechora Sea	12.00	10.00	5.50	0.38	0	0	0
2018	D2	A.m_25	Pechora Sea	10.00	9.50	5.00	0.21	0	0	0
2018	D2	A.m_26	Pechora Sea	10.00	9.50	5.00	0.26	0	0	0
2018	D2	A.m_27	Pechora Sea	10.50	10.00	5.00	0.30	0	0	0
2018	D2	A.m_28	Pechora Sea	10.50	10.00	5.00	0.29	2	0	0
2018	D2	A.m_29	Pechora Sea	10.50	10.00	5.00	0.26	0	0	0
2018	D2	A.e_03	Pechora Sea	12.50	10.00	4.00	0.27	1	0	0
2018	D2	A.m_30	Pechora Sea	10.50	10.00	5.50	0.29	0	0	0
2018	MSLP2	S.g_08	Pechora Sea	47.00	40.00	24.00	15.98	0	0	0
2018	MSLP2	S.g_10	Pechora Sea	48.00	44.00	25.00	17.11	0	0	0
2018	MSLP2	N.p_04	Pechora Sea	17.00	10.00	6.00	0.48	1	0	0
2018	MSLP2	M.g_1	Pechora Sea	5.00	9.00		0.27	0	0	0
2018	MV2	A.b_06	Pechora Sea	43.00	33.00	15.00	16.74	0	0	0
2018	MV2	A.b_21	Pechora Sea	46.00	35.00	15.00	17.07	0	0	0
2018	NW1	A.b_04	Pechora Sea	40.30	30.50	15.00	11.83	0	0	0
2018	NW13	N.m_03	Pechora Sea	11.50	12.00	6.00	0.66	0	0	0
2018	NW13	N.m_04	Pechora Sea	19.00	15.50	6.00	1.09	0	0	0
2018	NW13	N.m_05	Pechora Sea	23.50	22.00	10.00	3.93	0	2	0
2018	NW13	Y.h_08	Pechora Sea	20.00	10.00	5.50	0.61	0	0	0
2018	NW7	A.b_02	Pechora Sea	32.00	26.50	12.50	n/a	0	0	0
2018	NW8	N.p_01	Pechora Sea	-	-	-	-	-	-	-
2018	NW8	A.b_15	Pechora Sea	31.00	25.00	12.00	7.03	0	0	0
2018	NW8	A.b_16	Pechora Sea	32.00	29.00	14.00	8.93	0	0	0
2018	NW8	A.b_17	Pechora Sea	13.00	10.00	5.50	0.41	3	0	0
2018	NW9	A.b_25	Pechora Sea	42.00	35.00	21.00	15.50	2	1	0
2018	NW9	C.c_22	Pechora Sea	40.00	35.00	23.00	13.50	0	0	0
2018	NW9	C.c_23	Pechora Sea	30.00	32.00	20.00	7.40	0	0	0
2018	NW9	A.b_26	Pechora Sea	31.00	30.00	15.00	9.50	0	0	0
2018	NW9	A.b_27	Pechora Sea	33.00	26.00	12.00	6.10	1	0	1
2018	NW9	A.b_28	Pechora Sea	32.00	22.00	13.50	7.39	0	0	0

Year	Sampling site	Specimen ID	Research area	L, mm	W, mm	H, mm	Weight, g	MP, n		
								DGS	MC	G
2018	NW9	A.b_29	Pechora Sea	27.00	23.00	10.00	4.51	0	0	0
2018	NW9	A.m_16	Pechora Sea	15.00	13.00	8.50	0.82	1	0	0
2018	NW9	A.m_17	Pechora Sea	10.00	8.50	5.00	0.23	1	0	0
2018	V1	C.c_02	Pechora Sea	50.00	48.00	27.00	n/a	3	0	0
2018	V1	C.c_03	Pechora Sea	46.00	44.00	27.00	n/a	0	0	0
2018	V1	A.b_22	Pechora Sea	35.00	30.00	13.00	8.18	0	0	0
2018	V1	N.m_08	Pechora Sea	21.00	19.00	10.00	2.39	1	0	0
2018	V1	N.m_09	Pechora Sea	24.00	20.00	10.50	3.32	0	0	0
2018	V1	N.m_10	Pechora Sea	19.00	15.00	7.50	1.29	0	1	0
2018	V1	N.m_11	Pechora Sea	12.00	9.00	7.00	1.07	0	0	0
2018	V1	M.c_41	Pechora Sea	18.50	10.00	7.50	0.76	0	0	0
2018	V1	M.c_42	Pechora Sea	13.00	10.00	4.00	0.19	0	0	1
2018	V1	M.c_43	Pechora Sea	10.00	7.00	3.50	0.09	1	0	0
2018	V1	A.e_02	Pechora Sea	11.50	10.00	5.50	0.37	2	0	0
2018	V1	N.m_12	Pechora Sea	20.50	14.50	8.00	0.77	1	0	0
2018	V1	N.m_13	Pechora Sea	11.50	10.00	5.50	0.35	0	0	0
2018	V1	N.m_14	Pechora Sea	14.50	12.00	6.00	0.52	0	0	0
2018	V1	Y.h_30	Pechora Sea	20.00	8.50	4.50	0.17	0	1	0
2018	V1	S.g_09	Pechora Sea	9.50	8.00	5.00	0.15	0	1	0
2018	V1	N.p_02	Pechora Sea	15.00	8.50	5.00	0.24	0	0	0
2018	V2	A.b_01	Pechora Sea	39.00	32.00	15.50	n/a	1	0	0
2018	V2	M.e_01	Pechora Sea	38.00	20.50	15.00	3.70	1	1	0
2018	V2	C.c_18	Pechora Sea	26.00	25.00	16.00	3.53	0	0	0
2018	V2	C.c_19	Pechora Sea	16.00	15.00	10.00	1.17	0	0	0
2018	V2	C.c_20	Pechora Sea	17.00	15.00	10.00	0.78	0	0	0
2018	V2	C.c_21	Pechora Sea	25.00	23.00	15.00	2.64	0	0	0
2018	V2	S.g_11	Pechora Sea	27.00	23.00	15.00	2.89	0	0	0
2018	V2	S.g_12	Pechora Sea	15.00	13.50	9.00	0.73	1	0	0
2018	V2	S.g_13	Pechora Sea	15.00	16.00	8.00	0.68	0	0	0
2018	V2	A.e_04	Pechora Sea	10.00	8.00	4.00	0.21	0	0	0
2018	V2	A.e_05	Pechora Sea	8.50	7.50	4.00	0.15	0	0	0
2018	V2	A.m_31	Pechora Sea	10.00	10.00	5.00	0.31	0	0	0
2018	V2	A.m_32	Pechora Sea	10.00	9.50	5.50	0.26	0	0	0
2018	V2	A.m_33	Pechora Sea	8.00	7.50	4.80	0.13	1	0	0
2018	V2	A.m_34	Pechora Sea	9.00	8.50	4.80	0.13	0	1	0
2018	V2	A.m_35	Pechora Sea	8.50	8.00	5.00	0.13	0	0	0
2018	V2	A.m_36	Pechora Sea	7.50	7.00	5.00	0.13	0	0	0
2018	V2	A.m_37	Pechora Sea	5.50	5.20	4.80	0.09	1	0	0
2018	V2	A.m_38	Pechora Sea	7.50	7.20	4.80	0.11	1	0	0
2018	V2	A.m_39	Pechora Sea	8.00	7.50	4.80	0.13	1	0	0
2018	V2	A.m_40	Pechora Sea	8.00	5.50	4.80	0.12	0	0	0
2019	6537	P.a_37	Kara Sea	19.50	13.20	10.50	1.07	0	0	0
2019	6537	P.a_39	Kara Sea	20.00	13.00	9.50	0.97	0	0	0
2019	6473	M.e_02	East Siberian	50.00	25.00	15.00	5.70	0	0	1
2019	6473	M.e_03	East Siberian	47.00	22.00	12.00	3.87	1	0	0
2019	6473	P.a_21	East Siberian	14.90	10.00	5.50	0.40	0	0	0
2019	6473	P.a_22	East Siberian	13.00	10.50	8.00	0.66	0	0	0
2019	6473	P.a_23	East Siberian	15.00	10.00	5.50	0.35	0	0	0
2019	6490	P.a_27	Laptev Sea	10.00	8.80	5.20	0.21	0	0	0
2019	6490	P.a_28	Laptev Sea	10.00	6.00	4.80	0.09	0	0	0
2019	6490	P.a_29	Laptev Sea	10.10	8.50	5.00	0.14	0	0	0
2019	6490	P.a_30	Laptev Sea	9.80	6.80	5.00	0.10	0	0	0

Year	Sampling site	Specimen ID	Research area	L, mm	W, mm	H, mm	Weight, g	MP, n		
								DGS	MC	G
2019	6490	P.a_31	Laptev Sea	10.00	7.50	5.20	0.17	0	0	0
2019	6490	P.a_32	Laptev Sea	10.00	7.50	5.00	0.12	1	0	0
2019	6490	P.a_33	Laptev Sea	10.00	7.50	4.90	0.11	1	0	0
2019	6490	P.a_34	Laptev Sea	10.80	8.00	5.00	0.14	0	0	0
2019	6490	P.a_35	Laptev Sea	10.00	6.50	4.80	0.09	0	0	0
2019	6490	M.c_53	Laptev Sea	20.00	15.00	5.00	0.31	0	0	0
2019	6506	A.b_37	Laptev Sea	25.00	20.00	7.50	2.19	1	1	0
2019	6506	A.b_38	Laptev Sea	27.00	21.00	8.50	2.96	0	0	0
2019	6506	M.c_54	Laptev Sea	33.00	21.00	11.00	2.83	1	0	0
2019	6506	N.p_05	Laptev Sea	24.00	19.00	6.00	1.06	0	0	0
2019	6537	P.a_24	Kara Sea	19.00	10.50	8.80	0.74	0	0	0
2019	6537	P.a_25	Kara Sea	21.50	14.00	10.00	1.07	0	0	0
2019	6537	P.a_26	Kara Sea	22.00	13.00	8.50	1.24	0	0	0
2019	6537	M.c_51	Kara Sea	25.00	19.00	6.00	1.15	0	0	0
2019	6537	M.c_52	Kara Sea	32.00	25.00	11.50	3.89	4	0	0
2019	6537	P.a_36	Kara Sea	20.00	13.00	10.00	0.94	1	0	0
2019	6537	P.a_38	Kara Sea	20.00	13.50	10.00	1.08	0	1	0
2019	6537	P.a_40	Kara Sea	20.00	12.50	8.80	0.70	0	0	0
2019	6539	P.a_1	Kara Sea	17.50	11.00	6.00	0.48	2	0	0
2019	6539	P.a_2	Kara Sea	15.00	10.00	5.50	0.38	1	0	0
2019	6539	P.a_3	Kara Sea	13.00	11.00	6.50	0.52	0	0	0
2019	6539	P.a_4	Kara Sea	18.00	11.00	6.00	0.50	0	0	0
2019	6539	P.a_5	Kara Sea	16.00	11.50	6.00	0.43	0	0	0
2019	6539	P.a_6	Kara Sea	18.00	12.00	6.50	0.65	1	0	0
2019	6539	P.a_7	Kara Sea	15.00	10.00	5.50	0.38	0	0	0
2019	6539	P.a_8	Kara Sea	15.00	10.00	6.50	0.48	0	0	0
2019	6539	P.a_9	Kara Sea	15.80	10.00	6.00	0.46	0	0	0
2019	6539	P.a_10	Kara Sea	15.50	10.50	6.50	0.50	2	0	0
2019	6539	P.a_11	Kara Sea	18.00	12.50	7.50	0.61	0	0	0
2019	6539	P.a_12	Kara Sea	14.00	10.00	5.80	0.35	1	0	0
2019	6539	P.a_13	Kara Sea	20.50	10.00	6.00	0.42	0	0	0
2019	6539	P.a_14	Kara Sea	19.00	10.00	6.00	0.39	0	0	0
2019	6539	P.a_15	Kara Sea	14.50	10.00	5.20	0.32	0	0	0
2019	6539	P.a_16	Kara Sea	17.00	10.00	8.00	0.54	0	0	0
2019	6539	P.a_17	Kara Sea	15.50	11.00	5.50	0.33	1	0	0
2019	6539	P.a_18	Kara Sea	15.00	10.00	6.00	0.36	0	0	0
2019	6539	P.a_19	Kara Sea	15.00	10.00	6.00	0.34	0	0	0
2019	6539	P.a_20	Kara Sea	15.50	10.00	6.00	0.42	0	0	0